ENEMY RECOGNITION AND RESPONSE IN NEW ZEALAND ROBINS

A thesis submitted in

partial fulfilment of

the requirements for the

Degree of

Master of Science in Zoology

by

RICHARD F. MALONEY

University of Canterbury

1991

"...the birds never seemed to realise their danger...we may infer what havoc the introduction of any new beast of prey must cause in a country, before the instincts of the indigenous inhabitants have become adapted to the stranger's craft or power."

Charles Darwin, *Voyage of the Beagle*, 1845

"...if only the bird knew its powers, it wouldn't fall such easy prey to stoats...but he has no idea of attack or defence."

Charlie Douglas, *The birds of South Westland*, in the 1860's

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

Table Page

LIST OF APPENDICES

ABSTRACT

The ability of robins, *Petroica australis*, to recognise and learn about a mammalian predator (stoat, *Mustela erminea*) was studied during the 1989 and 1990 robin breeding seasons, on Motuara Island (no stoats present) and at Kowhai Bush, Kaikoura (stoats present).

I quantified the natural nest-defence responses of robins towards the stoat and a non-threatening control (a box) in both study areas. In the mainland population, all behaviours measured were given at greater rates by robins faced with the stoat compared to the box. In contrast, island robins responded about equally to the stoat and box, and at a level that was similar to the responses of mainland robins towards the box. These results suggest that mainland robins have learned to recognise and respond to stoats as enemies, and that the low nest-defence responses of the inexperienced robins may be typical of the responses of New Zealand endemic birds prior to the arrival of mammalian predators.

I trained robins on Motuara Island to respond to a stoat as an enemy using an artificial training technique, and tested their response one day later. All robins trained using conspecific training regimes gave nest-defence responses to the stoat at a level significantly higher than robins either not trained, or trained using an interspecific regime. Training using robin mounts and alarm calls, or just robin alarm calls resulted in the highest learned response, whereas training using distress calls resulted in an intermediate learned response. These results indicate that artificial training of birds in field situations may be an effective way to improve enemy recognition ability and enhance nest-defence responses.

I attempted to test the ability of robins to transfer nest-defence behaviours between generations by cultural transmission, but survival of robins was very low between seasons and insufficient data were collected to answer this question.

The intensity of response of robins towards the stoat at each nest was compared with six context-related variables. Of 63 comparisons only two were significantly correlated, suggesting that the intensity of robin nest-defence responses were not dependent on these context-variables.

CHAPTER 1

GENERAL INTRODUCTION

In many species of animal, parents use a variety of techniques to protect their young from predators and thereby increase the offsprings' chance of survival (Edmunds 1974, Morse 1980, Alcock 1984). Protection may include behaviours of the parent which prevent detection (eg. crypsis) or capture of offspring (eg. distracting, mobbing or attacking a predator). Such behaviours will be more effective if the parent is able to recognise the predator, as less time and energy will be wasted by the parent responding to non-threatening animals, or giving inappropriate responses to threatening animals. Many studies have found evidence that animals are able to recognise predators (eg. in birds, Altmann 1956, Armstrong 1954, Caldwell & Rubinoff 1983, Curio 1975, Klump & Shalter 1984, Nice & Pelkwyk 1941, Smith *et al.* 1984; in mammals, Hauser 1988, Hirsch & Bolles 1980, Robinson 1980, Seyfarth & Cheney 1990), and it is likely that the ability to recognise predators is a general phenomena among the higher vertebrates.

In some species, effective nest-defence responses are given to a novel predator on the first encounter, indicating that the ability to recognise predators may be genetically inherited (Curio 1975, Hobson *et al.* 1988, Mueller & Parker 1980, Owings & Coss 1977, Riechert & Hedrick 1990), whereas in others, recognition of predators may be learned (Coleman 1987, Conover 1987, Curio *et al.* 1978a, 1978b, Hauser 1988, Klopfer 1957, Knight 1984, Pugesek 1983, Regelmann & Curio 1983, Thornhill 1989, Vieth *et al.* 1980). It may be that inheritance of predator recognition involves a mix of genetic and cultural processes, where an animal is genetically predisposed to learn defence responses. This association between genetic and cultural heritability ("gene-culture transmission", Lumsden *et al.* 1981), has recently been modelled by Findlay (1991). Findlay (1991) derives a general theorem of natural selection based on genetic and cultural transmission and suggests that traditional, purely genetic models (eg. Fisher 1930) are a special case of gene-culture transmission.

Clearly, recognition of predators is fundamental to the anti-predator

behavioural strategies of many animals. In birds one such strategy, nest-defence behaviour, is particularly well-developed and appears to function as a response to protect a parents' nest and nest-contents against predation, although alternative functional hypotheses have been suggested (eg. as an advertisement of male quality, Regelmann & Curio 1986, see Curio 1978 for hypotheses).

I define *nest-defence behaviour* as "any behaviour that decreases the probability of a predator harming the nest or its contents while increasing the probability of harm to the parent". This definition is broader than that of Montgomerie & Weatherhead (1988, p.190) and includes harm to the nest itself, since effective defence of the nest structure may have significant time and energy cost savings. Non-costly nest-defence behaviours (eg. choosing a cryptic nest-site) are not included in this definition; a parent may perform non-costly behaviours without necessarily recognising, or having direct contact with the predator.

Nest-defence behaviours are risky to perform, with an increased chance of injury when attacking or distracting a predator (Brunton 1986, Curio & Regelmann 1986, Denson 1979, England 1986, Hammerstrom 1957, Myers 1978, Pettingill 1976, Poiani & Yorke 1989, Walker 1983, but see Hennessy 1986). However, evidence of risk of injury to the parent during nest-defence does not necessarily show that nest-defence has benefits in terms of increased offspring survival. This link is now clearly established, with a correlation between strong nest-defence responses and increased nest success having been found for many birds (eg. Andersson & Wiklund 1978, Andersson *et al.* 1980, Blancher & Robertson 1982, Buitron 1983, Byrkjedal 1987, Gottfried 1979, Greig-Smith 1980, Knight & Temple 1986a, Murphy 1983, Nichols *et al.* 1984, Pettifor 1990, Temrin & Jakobsson 1988, and see review in Montgomerie & Weatherhead 1988); although some studies have found no such correlation (eg. Smith *et al.* 1984).

Recognition of and response to predators by birds is clearly a complex behavioural process, with species having differing abilities at distinguishing among predator types, and also having different (and dynamic) responses (eg. Chandler & Rose 1988). However, the underlying mechanisms that birds use to determine level of nest-defence responses are not clear. Most recent studies have attempted to fit observed nest-defence responses to models based on parental investment theory (an

optimality-based theory, Trivers 1972; see Montgomerie & Weatherhead 1988, Redondo 1989 for reviews of theoretical models and evidence). In this theory, the pattern of nest-defence responses over a breeding cycle is predicted to be dependent on the parents future gain in reproductive fitness, which is most often measured as the time to offspring independence. Therefore, the intensity of defence by the parent increases as offspring grow older, as the expectation of future benefit to the parent increases while the cost of defence remains relatively constant. The pattern may also vary as future costs of raising offspring decrease, or as the difference between the cost of raising the current brood increases relative to future broods.

Evidence in support of the parental investment hypothesis is limited, with the pattern of nest-defence intensity not consistently fitting the predicted pattern in many birds (see McLean & Rhodes 1991), although in some studies the theoretical predictions about pattern of nest-defence intensity were supported (see Redondo 1989). Methodological problems with stimulus (ie. potential enemy or non-threatening object) presentation techniques, where the same stimulus is presented several times at one nest causing reinforced or habituated responses, may have contributed to differences in response intensity and pattern in some studies (Knight & Temple 1986b).

Studies that did not find evidence to support parental investment theory often suggest that the pattern of nest-defence response was hidden by variation in response intensity due to the context of the predator-defender interaction (eg. Hobson *et al.* 1988). Context-variables known to influence the intensity of nest-defence include variability resulting from differences inherent to the bird, nest or predator. These variables are reviewed by Montgomerie & Weatherhead 1988 and Redondo 1989 (and see Chapter 5).

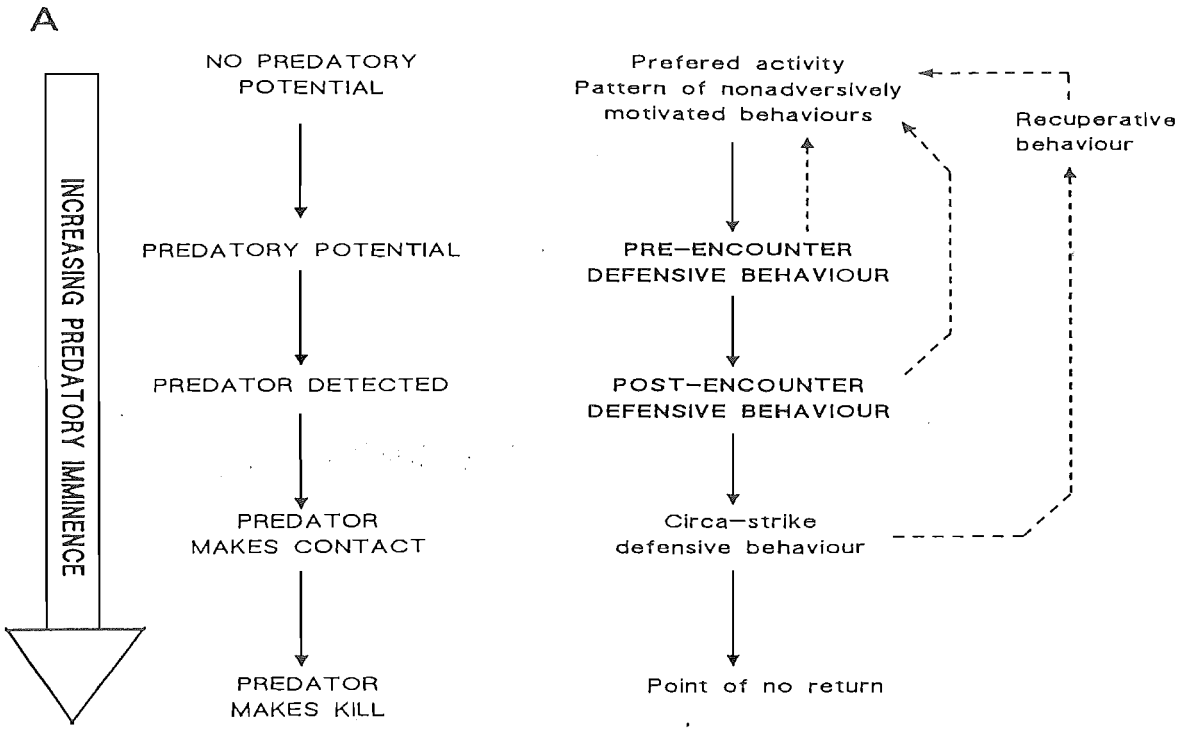
Regardless of the underlying theories which make predictions about the pattern of nest-defence responses, a bird defending its nest may need to process a large amount of information about the enemy stimulus, and should base its nest-defence decisions on that information. During each encounter with an enemy the bird needs to be able to react with a type of response, and at an intensity level, that is appropriate to the type of enemy, to the threat it poses to the offspring, and to the

danger of being injured during the encounter.

There are several general models which illustrate possible pathways through which the information received from the stimulus is processed (eg. Dörner 1982, Klix 1982, Lüer 1982, Markl 1985, Smith 1977, Toates 1983). These models generally follow a similar pattern of information-processing where, first, an image is perceived by sensory receptors, then processed, stored, and possibly matched to previously stored images. Next, decisions on suitable responses (which may be innately programmed) are made and the response is actioned. Finally, the modified situation brought about by the response is monitored (eg. see Smith 1977). Most variation among the theoretical models is in the degree of innate compared to learned input in the image processing, and in the presence of possible feed-back loops or guides which modify the recognition and response decision-making process along the information-processing pathway (eg. see Dawkins & Krebs 1978).

Two recent theoretical models provide outlines of possible cognitive pathways that prey may use in behavioural interactions with predators.

First, in the Predatory Imminence Continuum model (PIC, Fig 1.1a), the intensity and type of defence response given by the prey is viewed as being positively related to the distance (physical and psychological) from an approaching predator (Fanselow & Lester 1988). "Prey", as described in Fig 1.1a, applies to the parent bird as the actor, but for nesting birds that are protecting offspring the model may be broadened to incorporate relationships such as between parents (the defenders) and young (the direct beneficiary of the parent's behaviour). In the PIC model the parent "prefers" to remain at a point where it is safest from predation, and at this point it displays "non-adversively motivated behaviours" (eg. normal feeding activities). Before the prey has encountered the predator, the parent may also adopt what Fanselow & Lester term "pre-encounter defensive behaviours". These are actions that enable the parent to avoid future contact with the predator (eg. nesting in concealed or inaccessible sites). After encountering the predator, the parent must adopt new strategies which are designed to return the parent to its preferred motivation state. The strategies illustrated by Fanselow & Lester were, for example, freeze, hide or run responses of prey, which reduced the risk of contact with the predator.



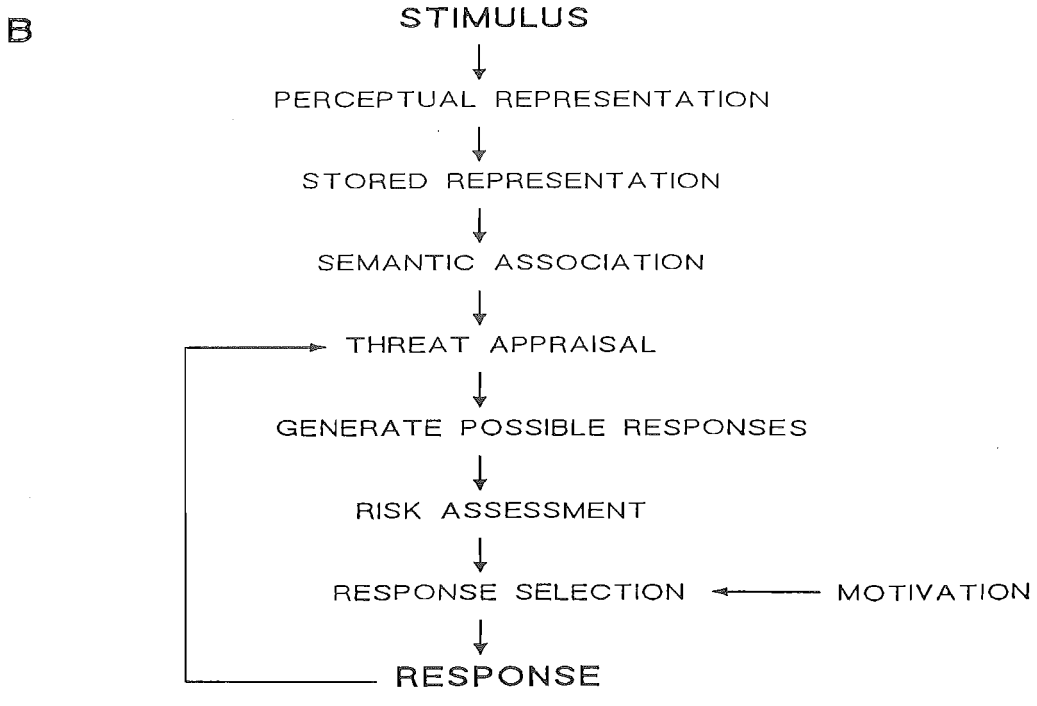


Figure 1.1: Theoretical models of enemy recognition and response in birds. A) The Predatory Imminence Continuum (PIC) model, after Fanselow & Lester (1988). B) A simple model of enemy recognition and response, after McLean & Rhodes (1991).

Nest-defence behaviours (which may include attacking or distracting the predator) may be considered appropriate strategies at this stage if the offspring in the nest are at imminent risk of injury, and given that running and hiding are not options for altricial young.

The PIC model provides an important theoretical base for developing predictions about the response of birds towards an enemy stimulus. The model predicts that defence responses are designed to allow a bird to return as quickly as possible (or with minimal injury) to a preferred motivational state. Thus level and type of response are directly determined by the imminence of attack from the predator.

The second theoretical model, the cognitive model of enemy recognition (McLean & Rhodes 1991, Fig 1.1b), provides more detail on a decision-making pathway that may be used to generate appropriate and modifiable prey responses towards an enemy stimulus. In this model, the stimulus (predator) is perceived (eg. visually, audibly) and this image is matched with stored images in a recognition process. Importantly, this model also includes both assessment of, and feedback from, the predator, acknowledging that intensity of response towards a predator may be context-specific and involves a dynamic process of action, observation, assessment and reaction. In birds where recognition is innate, the stored representation in Fig 1.1b is genetically inherited, whereas in species where recognition is learned, the stored representation may require development and fine-tuning, gained through experience with the predator.

Most studies of recognition and response of birds to enemies have been conducted on continental land masses, on populations of birds that have evolved in environments with many different enemy types (eg. avian, reptilian, mammalian), and with a long historical period of coexistence between predator and prey (ie. millions of years). In such areas where there is constant contact with different predator types, many birds may have well-developed genetically-based stored representations of predators, or they may be able to make semantic associations between unknown predators with known predators that are in the same taxon group (eg. mammalian, avian). Because of this, there is little opportunity to measure the nest-defence responses of birds towards *truly* novel enemies, although many studies

attempt to do so (eg. Coss & Owings 1978, Curio 1975, Hobson *et al.* 1988).

Birds endemic to remote island groups may be more suitable subjects for measuring the nest-defence responses given towards novel enemies. In an island group such as New Zealand, there has been a long historical isolation of many endemic birds from one important enemy group, the predatory mammals (Atkinson 1985, Holdaway 1989, King 1984). These birds almost certainly have no past experience with *any* of the predatory mammals and therefore a mammalian predator is a novel stimulus at the taxon level. Mammalian predators have been introduced to some parts of New Zealand in the past 1000 years, with the most recent introductions being about 100 years ago (Atkinson 1973, 1985, King 1984). Thus, in New Zealand there are sympatric populations of conspecific birds that I predict may have a similar level of genetic recognition ability of predators, but have different abilities in recognising and responding to predators, due to differences in the birds recent experiences with mammalian predators.

This prediction has been quantitatively tested once previously. McLean & Maloney (1989, in prep) compared the behavioural responses of naive island and experienced mainland populations of endemic tits, *Petroica macrocephala*, towards avian enemies. They found that the experienced population responded to the avian enemies more intensely than did the naive population, whose response to the enemies was weak and confused. McLean & Maloney concluded that the difference in response intensity between the populations was most likely due to the recent experiences of the mainland tits with avian enemies. However, no study has quantitatively tested whether naive or experienced populations of New Zealand endemic birds can recognise or respond appropriately towards mammalian predators.

Similarly, no study has examined the importance of learning in determining recognition and response abilities of New Zealand birds towards *mammalian* predators. If wild populations of endemic New Zealand birds can learn to recognise and respond effectively to predators, then by providing naive birds with artificial experiences of nest-defence responses, it should be possible to teach them appropriate enemy recognition and response abilities.

Finally, if artificial training techniques are successful and birds can learn to

recognise a mammalian predator as an enemy, then I predict that these learned defence behaviours may be transferred between generations by cultural rather than genetic means.

Aims

In this thesis I aim to test the predictions that:

1) Endemic New Zealand birds that have experience with mammalian predators respond more intensely to a mammalian predator than naive bird populations.

2) Artificial training will enhance nest-defence responses of birds towards mammalian predators.

3) The transfer of learned nest-defence responses may be achieved by cultural transmission.

Specifically, in Chapter 2, I examine the role of genetic and experience components of enemy recognition used by an endemic New Zealand bird, the robin, *Petroica australis*, in its nest-defence responses against a predator, the stoat, *Mustela erminea*.

In Chapter 3, I test the ability of robins to learn nest-defence response behaviours by experiencing appropriate but artificial mobbing events, between a conspecific and a stoat.

In Chapter 4, I examine the possible role of cultural transmission in the transfer of enemy recognition and nest-defence response skills between robin generations.

Finally, in Chapter 5, I examine several context-specific variables that may influence the level of robin nest-defence responses, independently of differences due to the predator.

STUDY ANIMAL, STUDY SITES AND GENERAL METHODS

Study animal

The South Island robin is a medium sized (30-40g) insectivorous passerine, patchily distributed at moderate to low densities throughout South Island but in higher densities (up to 2.8pr/ha) on a few offshore islands. Robins form highly stable life-long pair bonds, are strongly territorial year round and lay one to four clutches per year. The cup-shaped nest is sited 0.1m-15m above ground level, typically in primary tree forks, fern crowns, large tree-trunk cavities or in the canopy. Only the female builds the nest and incubates the eggs, while the male provisions her. Both birds feed chicks and fledglings (Flack 1975, 1985, Fleming 1950, Oliver 1930, Powlesland 1980, unpubl. data).

Study sites

This study was conducted on two islands in Marlborough Sounds (Allports Island, 174°03'E, 41°14'S; Motuara Island 174°16'E, 41°06'S) and at one South Island mainland site (Kowhai Bush, 173°37'E, 42°23'S; Fig 1.2). Robins occur naturally at Kowhai Bush, but the island populations were established after 1973, when two pairs were transferred from Inner Chetwode Island (174°04'E, 40°54'S) to Motuara Island, and from Kowhai Bush to Allports Island (Flack 1974, 1977, Flack & Lloyd 1978). All study sites are floristically very similar. Forest composition and structure is relatively simple with kanuka, *Kunzea ericoides*, being the dominant tree species (Flack & Lloyd 1978, Hunt & Gill 1979, Walls 1983, unpubl. data).

The avian fauna of the island sites is dominated by two species. These are robins and bellbirds, *Anthornis melanura*, on Motuara Island and robins on Allports Island. There is a greater diversity of native and introduced passerines at Kowhai Bush (Hunt & Gill 1979, Walls 1983, unpubl. data).

The most noticeable difference between sites is in the diversity of mammalian predators in each area. The only carnivorous mammals present on the islands (mice, *Mus musculus*, on Allports Island and kiore, *Rattus exulans*, on Motuara Island, Flack & Lloyd 1978) were eradicated during the winters of 1989 and 1990 respectively, by the Department of Conservation.

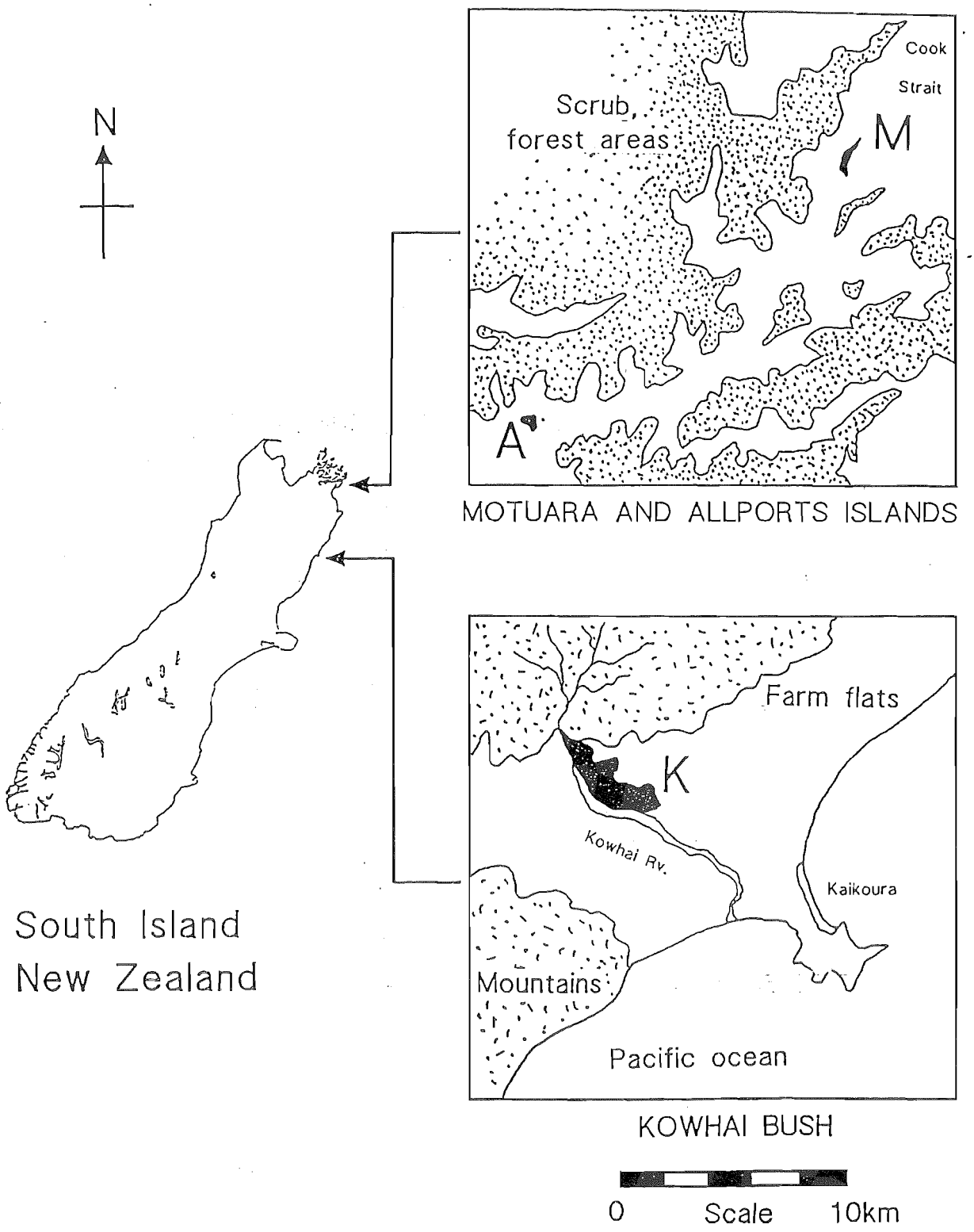


Figure 1.2: Location of Motuara Island (M), Allports Island (A) in Marlborough Sounds, and Kowhai Bush (K), Kaikoura, in South Island, New Zealand.

Kiore are the only mammal present on Chetwode Islands, the source island group for robins on Motuara Island. As far as is known, none of the other predatory mammals have ever established on these islands (R. Taylor pers. comm.). In comparison, Kowhai Bush has all of New Zealand's introduced predatory mammals except kiore; being stoats, ferrets, *Mustela furo*, weasels, *M. nivalis*, mice, Norway and ship rats (*Rattus norvegicus and R. rattus*, respectively) feral cats, *Felis catus* and hedgehogs, *Erinaceus europaeus* (Moors 1979, 1983).

Predation rates on robin nests are low on Motuara Island (26% average over 1973-75, 18% in 1989, 8% in 1990), low on Allports Island (13% average 1973-75, 4% in 1989) but are high at Kowhai Bush (55% average over 1971-76, all percentages from Flack & Lloyd 1978, unpubl. data).

General methods

Experiments at nests involved placing the stimulus (the stoat or the box) 1-1.5m from active robin nests. All robins were individually identifiable at the time of the experiment, either behaviourally, by mate or territory fidelity, or with individually-coded coloured leg bands. Appendices 1 and 2 describe the methods used for 1) finding nests and, 2) banding robins, and Appendix 3 details a list of banded robins and the experimental test each robin received.

Experiment design and data collection

To improve observer reliability in identifying and quantifying differences in robin behaviour, I spent 18 days at the beginning of this study on Allports Island, where I identified and became familiar with behavioural responses of robins towards the stimulus, finalized test procedures, and practiced and standardized test methods. None of these robins were used in further experiments.

From 18 tests (14 training attempts, 4 stoat and box trials) I identified seven major behaviour categories (body movements, calls, body displays), four appropriate measurements of time, and practised estimates of distance. These variables are defined in Table 1.1 and were used in all tests.

Table 1.1: Definition of measurements of behaviours, times and distance used throughout this study, and the source of previously described behaviours.

Behaviour or action of robin	Description of behaviour	Source
Body movements		
flights	Movements > one body length	
hops	Movements < one body length	
wing flicks	Rapid opening and closing of closing of both wings when perched	
Calls	Number and type of alarm and distress calls	Hay 1975
Body displays		
head feather displays	(a) display of frontal spot (b) display of raised head feathers	Flack 1976 & Powlesland 1980
wing droop display	Full distraction display	Powlesland 1980
Distances from stimulus (m)	>2m to nearest 0.5m <2m to nearest 0.1m	
Time Intervals (secs)		
time in view of stimulus	Preset to 5 min maximum	
natural times	Time between approaches to the nest prior to tests	
test times	Time between approaches to the nest during tests	
post-test times	Time between approaches to the nest after tests finished	

Natural approaches to the nest

I recorded behaviours and times (see Table 1.1) of parents returning to their nests prior to starting all tests. These data were used as a measure of baseline response levels and were compared to nest-approach data recorded during experimental trials. At least three natural approaches were observed for incubating females and four to nine approaches were recorded at nests containing chicks. Natural approach data were collected immediately after finding the nest, in the intervening days between when a nest was found and the first trial, or immediately prior to a sequence of trials.

I considered that a 'nest approach' began from when the robin ceased foraging and headed towards the nest. If I could not see a bird until it was flying towards the nest, then I considered that the approach began from where I first sighted the bird.

On all occasions that I made observations near robin nests, I sat 5-15m from the nest tree and I minimised my movement and disturbance of litter.

Presentation of stimuli

The stimuli (the stoat and box) were presented at nests of pairs of robins with chicks (Chapter 2) and the stoat was presented at nests of female robins with eggs (Chapters 3 & 4), using the following method:

(i) A string was thrown over a branch higher than the nest position, 1-1.5m from the nest rim and tied to form a continuous loop. The loop was positioned so that the stoat or the box attached across it faced the nest rim.

(ii) The stoat or box was attached to the strings and raised into view when the parents were away feeding, except when the nest was obscured from view (eg. high in the canopy). In this case the stoat or the box was attached to the strings at ground level and covered while the parent was still at the nest.

(iii) The stimulus was raised into view of the nest (in about 30-60 seconds) while the parent was absent from the nest area. When in position 1-1.5m from the nest, the stimulus was level with and faced towards the nest rim. I tugged twice on a string attached to the stimulus when the returning bird was first observed approaching the nest, which moved the stimulus in a consistant manner and

immediately attracted the bird's attention.

Response intensity score

Each behavioural variable was analysed separately, and I also developed a score measuring overall intensity of nest-defence response at each nest, using a subjective 0-2 scale. Eight of the behaviour, time and distance variables (Table 1.1) were scored using ranking criteria based on level of risk to the actor, degree of dissimilarity from normal feeding movements and behaviours, and comparison with observed responses of robins to real mammalian predators (Flack 1976, Hay 1975, Powlesland 1980, Soper 1972, unpubl. data).

Level of risk was assumed to increase greatly as an actor: (i) approached the stimulus, (ii) went to the nest while in view of the stimulus, or (iii) behaved in a manner which increased an actors conspicuousness (eg. alarm calling, some body displays, see Curio & Regelmann 1986). Therefore, trials where these actions occurred scored more highly than did trials where a bird exhibited actions more similar to feeding and general activity movements.

Robins in each trial scored 0, 1 or 2 for each behavioural variable, using the criteria given in Table 1.2. During normal natural approaches robins rarely alarm called or gave head feather displays and never gave wing-droop displays (in over 600 recorded nest approaches, unpubl. data). Therefore, the highest intensity scores for these behaviours were rated as being whenever the behaviour occurred one or more times. Overall, the minimum total score possible during a trial was 0 (score of 0 for each of the eight behaviour, time and distance categories) and the maximum score 16 (score of 2 for each category).

Table 1.2: Response intensity score for robin behaviours, times and distance measures. Descriptions of behaviours as for Table 1.1. See text for details of the criteria used for ranking behaviours.

Behaviour or action of robin	Intensity Score 0	1	2
Number of:			
-flights	≤ average for natural approach	>1 but ≤2 times natural approach	>2 times natural approach
-wing flicks			
-hops			
Goes to nest	within first 1 minute	after 1 minute but before test was over (5min)	after test was over (>5min)
Minimum approach distance	>1m	0.5-1m	<0.5m
Alarm calls	No	Once	>1
Head feather displays	No	Once	>1
Wing droop display	No	Once	>1

CHAPTER 2

Enemy recognition and response in robins

New Zealand has been free of many of the world's major predator groups for most of its geological history. The absence of ground-hunting predators such as mammals and snakes allowed many birds (the dominant vertebrate taxon) to occupy niches filled elsewhere by mammals (eg. Holdaway 1989, King 1984). The first terrestrial predatory mammals to arrive were the kiore, *Rattus exulans*, and kuri, *Canis familiaris*, brought by early Polynesian colonists about 1000 years ago. Although kuri probably did not range far from human habitation, it is thought that kiore quickly spread throughout New Zealand (Atkinson 1985, Holdaway 1989).

From Polynesian colonization to the time Europeans arrived in New Zealand in 1770, approximately 36 (22%) species of bird became extinct. Europeans introduced two other rat species (the Norway rat, *R. norvegicus*, and the ship rat, *R. rattus*), the feral cat, *Felis catus*, and three mustelids (stoats, *Mustela erminea*, weasels, *M. nivalis*, and ferrets, *M. furo*). In association with massive habitat destruction, these introductions added to the decline of the New Zealand avifauna (10 additional species became extinct, Holdaway 1989).

Predation prior to the arrival of mammals was by aerial predators, and in the absence of mammalian enemies many endemic New Zealand birds developed flightless and ground-living habits (see Pomeroy 1990 for an hypothesised function of flight to escape predators). With these characteristics and with probably weak behavioural defences, many species were unable to cope with the invasion of predatory mammals (Holdaway 1989, McDowall 1969, Williams 1962).

Several early naturalists commented on how the fearlessness and curiosity of many New Zealand birds made them easy prey for mammalian predators (Buller 1882, M'Lean 1911, Reischek 1930, Wilson 1877). However, only a few anecdotal accounts describe the behaviour of birds during first encounters with predatory mammals (eg. Gutherie-Smith 1925, Heaphy 1842, Morrell 1958, Reed & Reed 1969). Moors (1983) compared predation rates of endemic New Zealand species with rates for "mammal-adapted" bird species introduced by Europeans and found

that endemic species were not more susceptible to predation than were introduced species. However, Moors did not control for selection due to bird-predator interactions since the mammal introductions and, therefore, this study does not necessarily measure the susceptibility of endemic species to predation at the time of the mammalian introductions.

Today, several populations of endemic birds continue to live in isolation from mammalian predators (eg. on remote offshore islands such as the Snares Islands). Thus, the responses of completely naive birds towards mammalian predators can still be quantified and, in some instances, compared with responses given by conspecific populations coexisting with mammalian predators. However, no study has recorded the behaviour of endemic New Zealand birds towards any of the introduced mammalian predators prior to contact with that predator, although behavioural responses of naive and experienced tits, *Petroica macrocephala*, towards two avian enemies, the little owl, *Athene noctua*, and long-tailed cuckoo, *Eudynamys taitensis*, has been studied (McLean & Maloney 1989, & in prep). McLean & Maloney (1989) found that naive tits on the isolated Snares Islands responded in a weak and confused manner towards potentially threatening owl and cuckoo mounts compared to a non-threatening control stimulus, whereas experienced tit populations in mainland New Zealand responded strongly and directed nest-defence behaviours only towards the enemy stimuli.

That study provided important background information on the possible behavioural effects of temporal or spatial separation of birds from their enemies. Because of the New Zealand avifauna's long historical isolation from mammalian predators, I predict that birds would not have recognised mammalian predators as a threat during the initial period of contact. The aim of this chapter is to provide the first quantitative test of this prediction.

Specifically, I examine enemy recognition and nest-defence response in mammal-naive and mammal-experienced populations of an endemic New Zealand passerine, the robin, *Petroica australis*, towards an introduced mammalian predator, the stoat.

As a second aim I examine within population differences in nest-defence responses due to the sex and number of robins present during a stimulus presentation.

METHODS

General methods

A taxidermic mount of a mammalian predator (a stoat) and a non-predatory stoat-sized control (a cardboard box) were used in all tests of robin nest-defence responses, during the 1989-90 and 1990-91 robin breeding seasons on Motuara Island and at Kowhai Bush, Kaikoura. Each test consisted of two trials at one nest. A trial involved the presentation of a stimulus (the stoat or the box) at a nest, with the order of stimulus presentation randomly chosen for the first test and alternated thereafter.

The stoat mount was used to elicit robin nest-defence responses. Mounts of animals are frequently used in place of live predators and they represent a realistic and constant stimulus in all presentations (see Curio 1975). The box was used as a control for the stoat by providing a measure of response to any object placed near the nest.

Two observers carried out the tests using different stoats and boxes as robin breeding times overlapped between the study sites. I completed all 30 Motuara Island trials and eight of the Kowhai Bush trials. The remaining six Kowhai Bush trials were completed by Dr I.G. McLean following specific guidelines set by me. Dr McLean had observed similar trials on Allports and Motuara Islands in 1989 and was familiar with robin behaviour and my experimental procedure. All presentation strings (Chapter 1) were positioned by me.

Construction of stimuli

I constructed each of the stoats by taxidermically mounting a female stoat and wiring it along a 25mm diameter, 400mm long branch. Each box was constructed from cardboard, shaped to form a stoat-sized rectangular box (370mm long, 45 x 45mm, which was held together with masking tape. All stoat mounts and boxes had a short length of coiled wire at one end and two 150mm long wires at the other for attachment to strings (Fig 2.1).

Figure 2.1: The stoat mounts and boxes used as enemy stimuli in this study. The upper two stimuli were used in all island trials and training events, and in all but six of the Kowhai Bush trials.

Experimental procedure

Tests were carried out on robins at nests with 5-20 day old chicks, at any time of the day. Observations and trials at the same nest on different days were made during the same part of the day, with the interval between trials as near to 24 hours as possible. Robins used in this experiment had not been used in any other experiment.

Tests were conducted as follows:

Day One: Four to nine natural approaches to the nest of the test pair were recorded before attachment strings were placed in position (see Chapter 1).

Day Two: To allow the birds to become used to my presence, I quietly observed 1-3 feeding approaches to the nest by the test pair. When both birds were out of sight, I attached the first stimulus (the stoat or the box) to the strings and positioned it by the nest (as described in Chapter 1). A timed 5 min trial period began when either parent returned to the area and reacted to the presence of the stimulus (reaction to the stimulus was deemed to have occurred if the robin abruptly veered off its nest-approach flight path, or stopped and orientated towards the stimulus). For the duration of each trial period the movements and behaviours (Table 1.1) of the birds were spoken into a hand-held cassette tape-recorder (Sanyo M1001A). The stimulus was then removed and behaviours and times during the post-trial approach to the nest were noted.

Day Three: The second stimulus was presented in the same manner as on Day Two and robin nest-defence responses were recorded.

Comparisons

I used the overall intensity score and individual behaviour, times and distance measures (Table 1.1) to compare robin nest-defence responses towards the stoat and the box. Because of differences between each trial in the number and sex of robins present and because presentation order of stimuli was alternated, I compared the nest-defence responses given to each stimulus by (a) different numbers or (b) different sexes of robins and (c) I compared between responses where the stoat was presented before the box with responses where the box was presented first. Where such comparisons were not significantly different, I averaged

(a) and pooled data for (b) and (c).

Comparisons were then made between trials in:

1) response towards enemy and control stimuli *within* each study area and;

2) response towards enemy and control stimuli *between* study areas.

Analyses

Wilcoxon Sign Rank tests were used for paired data comparisons within each study area, Mann-Whitney U tests for unpaired comparisons between study areas and Chi-square tests for analysis of data on body displays and calls. Where one datum of a paired measurement was missing, that pair was excluded from the analysis.

RESULTS

Nest-defence responses of robins were measured at 30 nests on Motuara Island and 14 nests at Kowhai Bush. The number and sex of robins present at each trial is given in Table 2.1.

Table 2.1: Total number of stoat and box trials completed and the number of trials that (i) males and females, (ii) only males and, (iii) only females were present; at Kowhai Bush and on Motuara Island.

Location and trial type	♂ & ♀ both present	Only ♂ present	Only ♀ present	Total number of trials
Kowhai Bush				
Stoat Trials	11	0	3	14
Box Trials	8	2	4	14
Motuara Island				
Stoat Trials	16	7	7	30
Box Trials	15	9	6	30

Differences in response of robins due to number of birds present, sex of birds, and stimuli presentation order

Responses to each stimulus when two birds were present were not significantly different from two times the response level when one bird was present (Appendix 4a). Therefore, in all further analyses, I use the average response towards each stimulus for comparisons between trials where more than one bird was present.

There were no significant differences in response toward the stoat or box due to the sex of the robin present at each trial or due to the order of stimulus presentation, either on Motuara Island or at Kowhai Bush (Appendix 4b & c). Sex of the responding bird and order of presentation of the stimuli are not considered in further data analyses.

Analyses of the response of robins towards enemy and control stimuli

Results of all statistical tests are presented in Table 2.2.

Response intensity score

The average response intensity scores of robins to the stoat and the box in each study area are shown in Fig 2.2.

The response intensity scores for robins on Motuara Island (M) given towards the stoat (S) compared to the box (B) were not significantly different (ie. MS=MB). Nor was the response intensity of robins at Kowhai Bush (K) towards the box significantly different from either trial on Motuara Island (ie. KB=MB=MS). However, the response score given by robins at Kowhai Bush towards the stoat was significantly higher than Kowhai Bush box trials and Motuara Island stoat and box trials (ie. KS>KB=MB=MS).

Separate analysis of behavioural variables

When each of these behaviours was analysed separately, the pattern of response was similar to that found for the intensity score analysis.

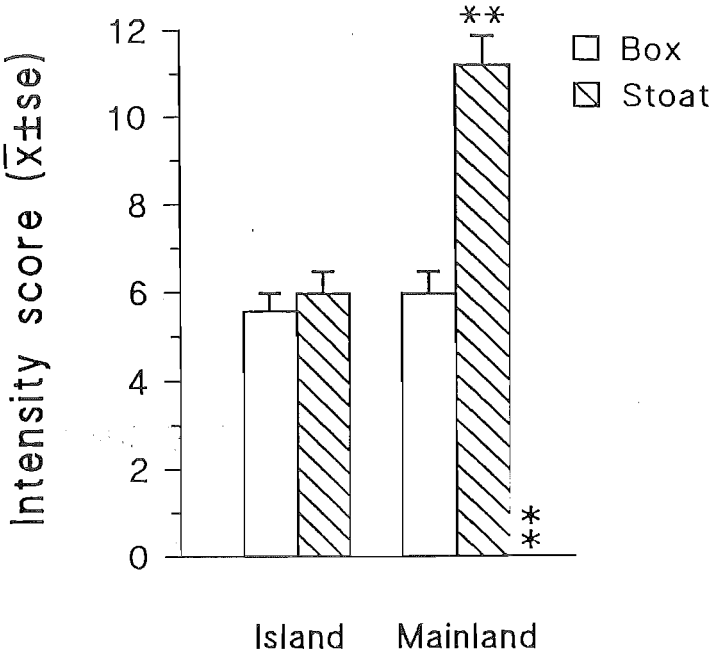


Figure 2.2: Mean (±se) response intensity score per trial by robins towards stoat and box on Motuara Island (N=30) and on the mainland (N=14). The intensity score is defined in Table 1.2, and in Chapter 1. The line under the x-axis at an equivalent level indicates pairwise comparisons that are not significantly different from each other at $p<0.01$. Asterisks above the bars show significant comparisons within study areas; asterisks beside bars show significant comparisons between study areas separately for stoat and box presentations. ** $p<0.01$.

Table 2.2: Statistical comparisons of the response of robins towards the stoat (S) and the box (B) on Motuara Island (M) and at Kowhai Bush (K).

	Stoat v Box#		Motuara Island v Kowhai Bush##			
Variable measured	MS v MB	KS v KB	MS v KS	MB v KB	MS v KB	MB v KS
Intensity score	NS	0.002	<0.001	NS	NS	<0.001
Flights	NS	0.047	0.012	NS	NS	0.003
Wing flicks	NS	0.003	0.009	NS	NS	0.003
Hops	NS	0.003	0.008	NS	NS	0.001
Closest approach	NS	NS	NS	NS	0.039	NS
Total time between feeds	NS	0.019	0.011	NS	NS	NS
Time off nest after seeing stimulus	NS	0.037	0.005	0.023	NS	0.023
Time to post-trial feed	NS	NS	NS	NS	NS	NS

Body displays+	X^2	df	p	Difference
	18.7	3	<0.001	KS>MS=MB=KB

\# = Wilcoxon Sign Rank tests
= Mann-Whitney U tests
\+ = Chi-square test

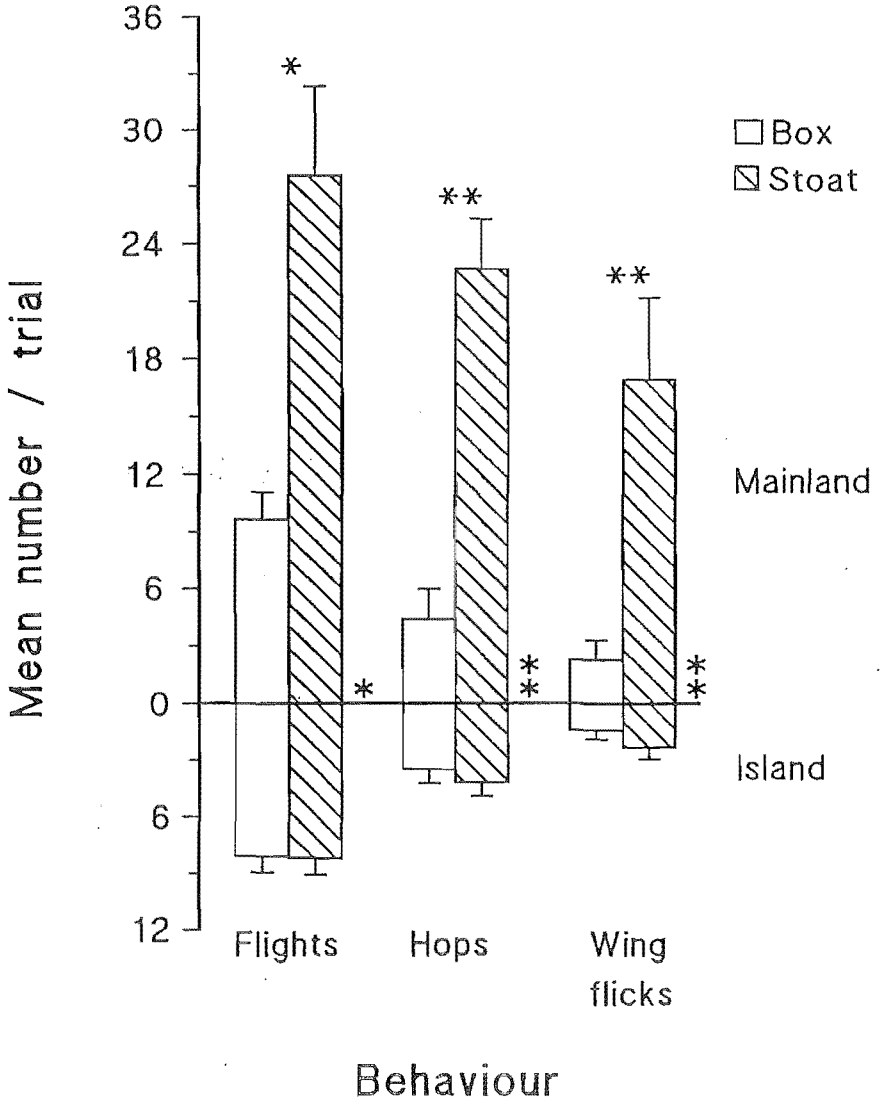


Figure 2.3: Mean (±se) number of flights, wing flicks and hops per trial by robins presented with the stoat and box, on Motuara Island (N=30) and on the mainland (N=14). Asterisks above the bars show significant comparisons within study areas; asterisks beside bars show significant comparisons between study areas separately for stoat and box presentations. * $p<0.05$, ** $p<0.01$.

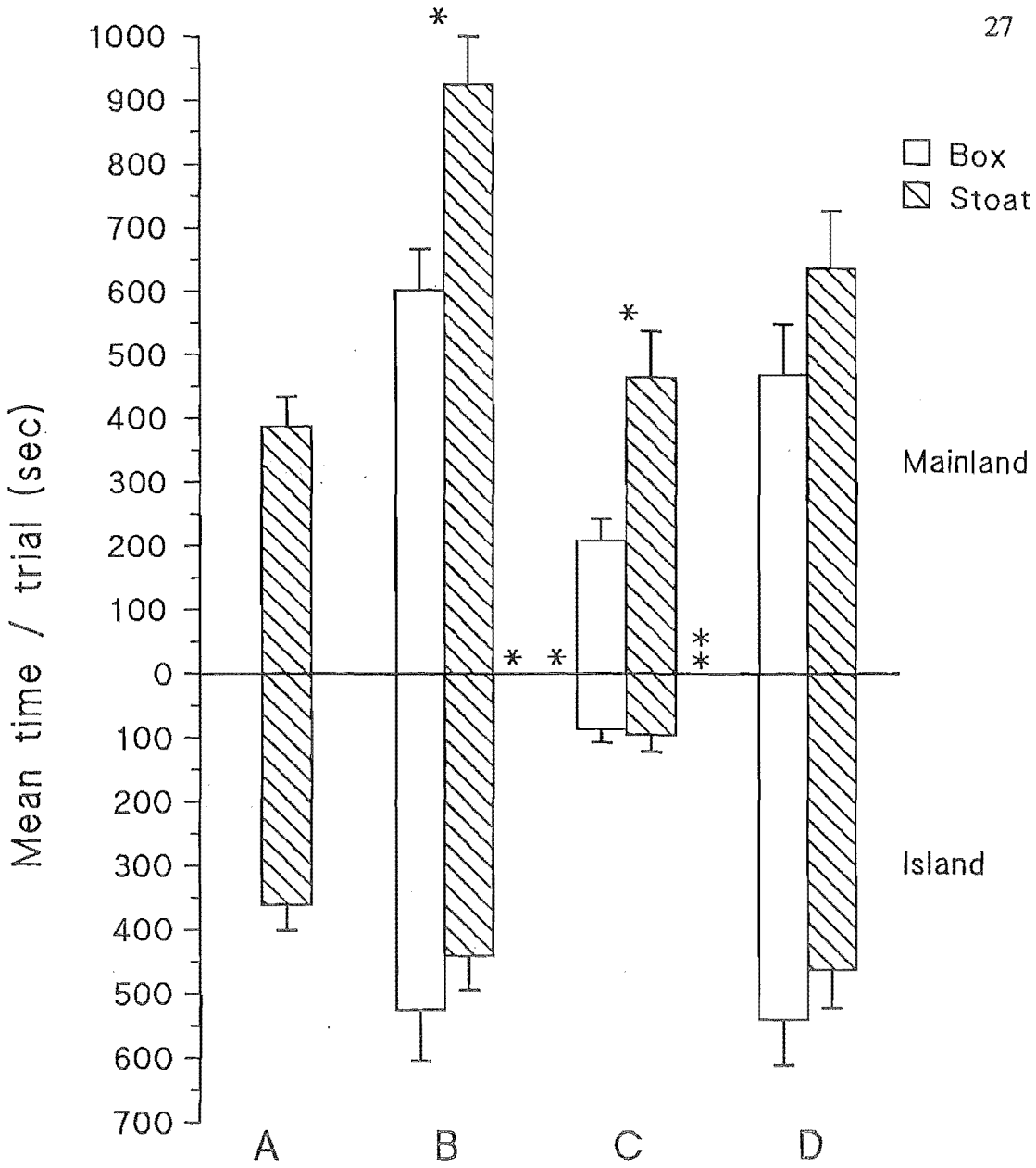


Figure 2.4: Mean (±se) time between feeds of the chicks per trial by robins presented with the stoat and box, on Motuara Island (N=30) and on the mainland (N=14). Times are A) natural time between feeds (pre-stimulus presentation); B) total time between feeds during a stimulus presentation; C) time from when a robin sights the stimulus to when the chicks are fed (a subset of B); and D) time to the first feed of the chicks after the stimulus was removed (post-stimulus presentation). Asterisks above the bars show significant comparisons within study areas; asterisks beside bars show significant comparisons between study areas separately for stoat and box presentations. * $p<0.05$, ** $p<0.01$.

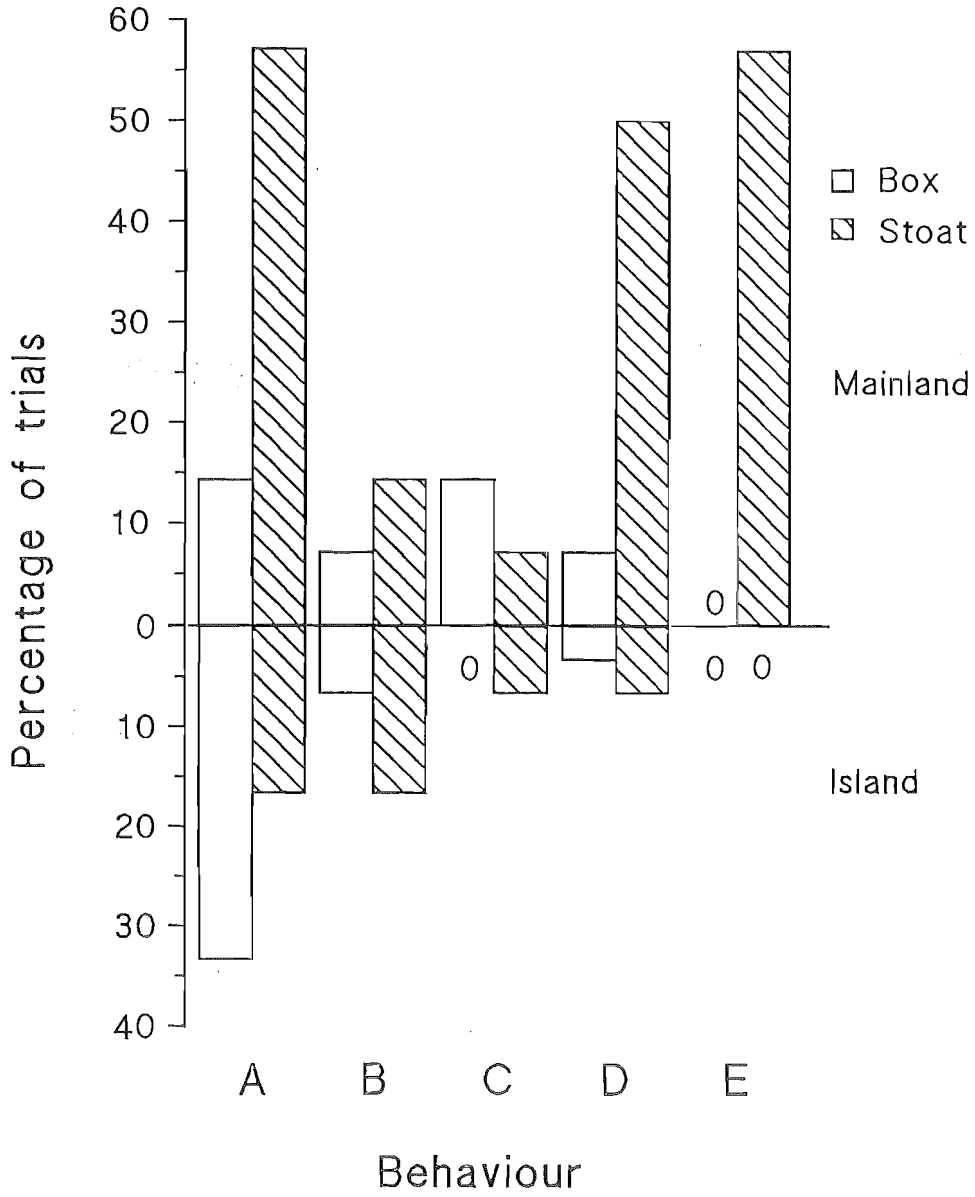


Figure 2.5: Frequency of stoat and box stimulus presentations during which robins gave A) wing droop displays, B) frontal spot displays, C) bill wiped, D) raised crown feathers, or E) alarm called or gave body displays, on Motuara Island (N=30) and on the mainland (N=14).

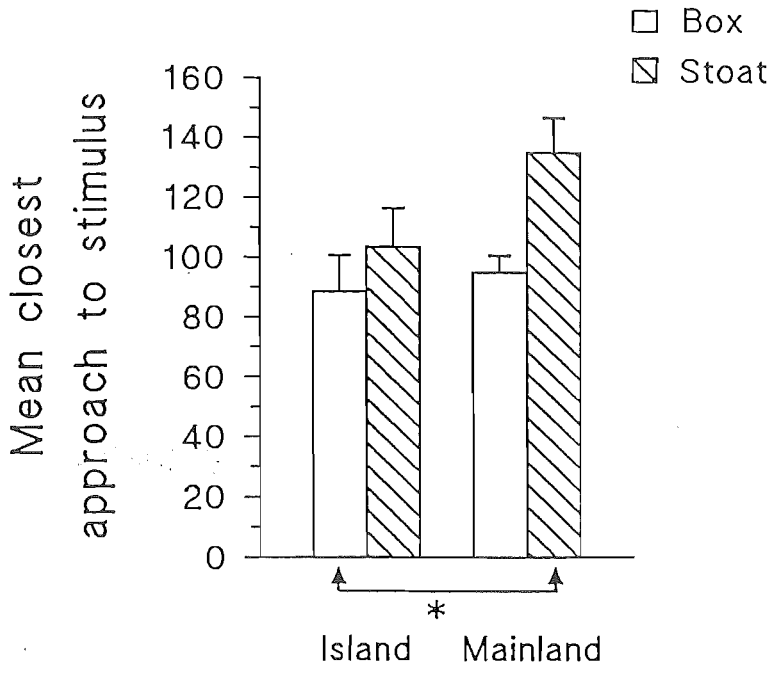


Figure 2.6: Mean (±se) closest approach distance by robins to the stoat and box per trial, on Motuara Island (N=30) and on the mainland (N=14). * shows $p<0.05$ for the comparison arrowed.

There were no significant differences in the response of robins towards the stoat compared to the box on Motuara Island for any of the behaviour, time or distance variables measured (ie. MS=MB). At Kowhai Bush, robins gave significantly more flights, hops and wing flicks (Fig 2.3), and took longer between successive feeds of chicks for the stoat compared to the box trials (ie. KS>KB, Fig 2.4). The increased time between feeds was because robins spent relatively more time away from the nest after sighting the stoat and was not a result of differences in foraging times prior to seeing the stoat.

Comparisons between study areas show that robins responding to the stoat at Kowhai Bush flew, wing flicked and hopped significantly more (Fig 2.3), took a longer total time between successive chick feeds and took longer to feed the chicks after sighting the stoat (Fig 2.4), than robins responding to either the stoat or the box on Motuara Island (ie. KS>MS=MB). However, none of the other variables (as described in Table 1.1) were significantly different between study areas for stoat trials (Fig 2.5 & 2.6), nor were between-area comparisons for any of the variables significant for box trials (ie. KB=MB=MS).

DISCUSSION

Differences in responses of robins due to the number of birds present, sex of birds, and stimulus presentation order

Robins responded to an enemy stimulus near the nest at a level which did not depend on the presence or absence of the mate, the sex of the bird present, or whether the robin had seen a non-threatening box in the same position the previous day.

In contrast, several studies have found that intensity of nest-defence differs between the sexes (eg. Curio 1975, 1980, Hobson *et al.* 1988, McLean 1987, Weatherhead 1979). Explanations of between-sex differences include unequal confidence of parenthood, differences in conspicuousness of the sexes or differences due to males advertising their quality (see Montgomerie & Weatherhead 1988, Regelmann & Curio 1986).

For a stable pair-bonded, monogamous and monochromatic species such as the robin (Powlesland 1980, unpubl. data), there may be advantages in sharing responsibility for nest-defence against predators. I suggest that both parents being able to defend their nest from predators will accrue advantages, first, in offspring protection by increasing the probability that either parent is in the nest area, and second, in foraging efficiency where both birds may spend longer foraging for food away from the nest area. Equal contribution to nest-defence may well be typical of other monogamous and strongly territorial birds (eg. Taylor 1991, in the rifleman, *Acanthisitta chloris*, and the grey warbler, *Gerygone igata*). The intensity of nest-defence by each robin does not change when the partner arrives possibly because both birds are already responding maximally towards that particular predator stimulus.

Responses of robins towards enemy and non-threatening stimuli

Robins at Kowhai Bush appeared to recognise the stoat near the nest as an enemy and responded with appropriate nest-defence behaviours. In comparison, Motuara Island robins did not appear to recognise the stoat and responded in a weak and confused manner. All of the behavioural variables support this conclusion, whether analysed individually, or collectively as an intensity score.

On Motuara Island low intensity behaviours such as body movements were given by robins equally to both stimuli, whereas body displays and alarm calling (ie. presumed high motivation nest-defence behaviours) were rarely and often inappropriately given. For example, wing-droop distraction displays were given to the box in twice as many trials as to the stoat and even the strongest nest-defence response usually concluded with the robin returning to the nest while the stimulus was still in position.

In comparison, Kowhai Bush robins responded intensely to the enemy stimulus. Responses towards the stoat involved a high number of body movements, high levels of alarm calling and frequent wing-droop distraction displaying. However, the box elicited nest-defence responses at a similar level to those recorded on Motuara Island. Kowhai Bush robins never returned to the nest while the stoat was in position, but frequently did so when the non-threatening box was near the nest.

The high levels of robin nest-defence responses recorded in the Kowhai Bush population are likely to be the result of experience with stoats, with predation by stoats causing selection pressure for effective nest-defence behaviours in Kowhai Bush robins. Robins on Motuara Island have no experience of stoats, and so there has been no selection for strong nest-defence behaviours.

I suggest that prior to the introduction of stoats, robin populations in New Zealand probably had nest-defence responses similar to those of the Motuara Island population.

CHAPTER 3

Enhancement of robin nest-defence behaviours by training

Although some studies have shown that animals may possess an innate ability to recognise predators (eg. Coss & Owings 1978, Curio 1975, Hirsch & Bolles 1980, Hobson *et al.* 1988, Mueller & Parker 1980, Riechert & Hedrick 1990), several other studies have found that a learning period is necessary for an animal to develop and hone recognition skills (eg. Coleman 1987, Conover 1987, Regelmann & Curio 1983, Thornhill 1989, see Chapter 1).

Birds that require experience with predators to develop effective anti-predator behavioural responses are at greater risk of injury than those who have genetic recognition and response abilities (Bolles 1970). However, some birds do not have the opportunity to experience appropriate defence-responses or have lost genetically-based abilities to respond appropriately to predators (McLean & Maloney 1989, in prep). These birds are particularly vulnerable to introductions of unrecognised predator groups.

The New Zealand avifauna evolved in an environment free from mammalian predators and was severely reduced when humans and other mammals arrived (Holdaway 1989, McDowall 1969, and see Chapter 2). One hundred years after the last of the major predatory mammal introductions three groups of birds are still naive about mammalian predators. The first are populations that live on offshore islands which are free from some or all mammals (eg. birds on the Snares and Rangatira Islands); the second are naive juvenile birds who have not yet learned anti-predator responses by experience; and the third are birds raised in captivity in the absence of predators, then released into the wild as part of captive-rearing and release management programmes (eg. takahe, *Notornis mantelli*, black stilt, *Himantopus novaezealandiae*, North Island weka, *Gallirallus australis*).

Vieth *et al.* (1980) have showed that individuals can be artificially trained in the laboratory to mob non-threatening objects, by giving them experiences watching another bird mobbing the object. Similarly, Ellis *et al.* (1977) have successfully trained coveys of masked bobwhites, *Colinus virginianus*, to remain in cover or to

flush, depending on the type of predator chasing them. However, Ellis *et al.* did not detail how the information was transferred between individuals in the covey and successful training may have relied as much on increasing the bird's flying ability as teaching them appropriate responses. There has been no application of a training technique to field situations, where naive birds are taught how to respond to a potential predator by watching the responses of other individuals, *before* contact with the predator is made.

The aim of this chapter is to test whether an artificial training technique can be used to enhance nest-defence behaviours in a field situation. Specifically, a population of robins are trained to give nest-defence responses towards a previously unknown predator, the stoat.

METHODS

General methods

Robins were trained to recognise and respond to an enemy near the nest by giving them an experience of an appropriate mobbing event (ie. an attack or distraction display by one or more individuals). A mobbing training event involved the stimulus of a conspecific giving a vocal and visual mobbing display towards a moving enemy (the stoat). Training occurred on Day 2 of the experiment. On the following day (Day 3) the stoat was presented 1-1.5m from each robin nest and nest-defence responses of the female were recorded using variables described in Table 1.1.

All training was undertaken on Motuara Island during the 1989 and 1990 breeding seasons, on robins at the incubation stage. None of these robins had been used in any other experiments.

Training procedure

Day One: Natural nest-approach data were recorded and attachment strings positioned by the nest for the Day 3 stoat presentation (see Chapter 1). The approximate location of territory boundaries were determined by observing the limits of a pair's foraging range and using knowledge of neighbouring pair boundaries (pers. obs.).

Day Two: Training mounts and speakers were set up on the ground as illustrated in Fig 3.1.

Figure 3.1: Training regimes used in this study, showing the mobbing bird mount, the stoat, and the speaker (partially hidden by litter directly behind the bird mount).

All training was conducted in a central area within the territory, and more than 10m from the nest. When the female left the nest to feed, the mounts were uncovered and the training event was run for 5 min. The criterion for beginning training was that the female be in line of sight of the training arena. To increase inter-nest consistency in starting conditions I did two things. First, I fed the male a small number of *Tenebrio* larvae. With the larvae the male called the female off the nest and often fed her within sight of the training arena. Second, if the male fed the female nearby but out-of-sight of the arena, I played a short 5-10 second burst of alarm calls through the speaker, which always attracted both birds into the training arena. During a 5 min training event I recorded responses of robins into a hand-held cassette recorder, after which the mounts were removed.

Day Three: Nest-defence responses of robins toward the stoat were recorded by placing the stoat by each nest on the strings positioned on Day 1. The behaviours, times and distance (Table 1.1) of the female returning to the nest were recorded.

Construction of mounts and playback recordings

A description of construction of the stoat mount is given in Chapter 2. The bird mounts used during training were:

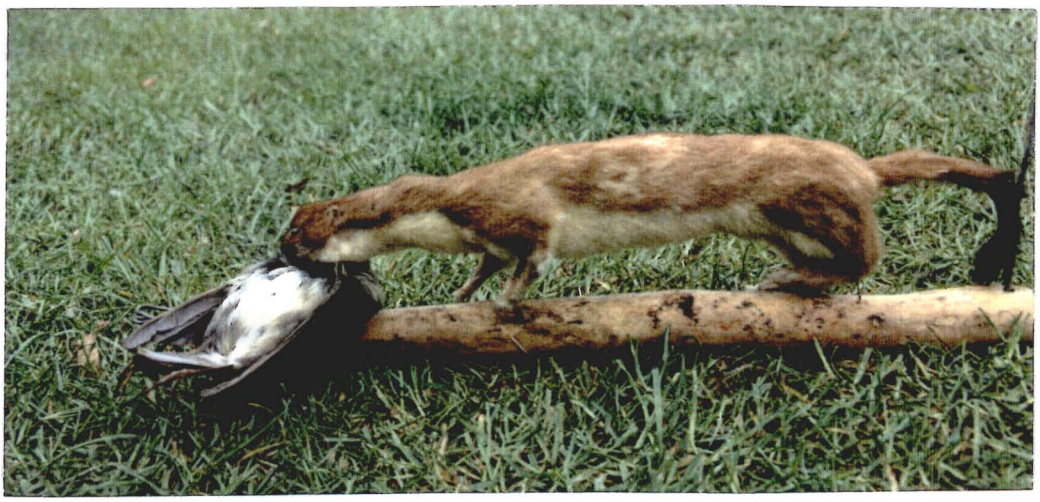
(i) Mobbing robin mount (Fig 3.2a). A female robin found freshly dead on Allports Island in October 1989 was taxidermically mounted with wings and tail spread and positioned on a 270mm long x 25mm diameter branch.

(ii) Robin in the stoat's mouth (Fig 3.2b). Two robins found dead on Allports and Motuara Islands were soaked in 70% alcohol for one week then air dried. The second robin was a replacement used in training events in November 1990.

(iii) Mobbing blackbird mount (Fig 3.2c). An immature male blackbird, found dead in the University of Canterbury grounds, was prepared by removing the viscera, mounting the bird on a 150mm long x 20mm diameter branch and freeze-drying for 48 hours.

A)

B)



C)

Figure 3.2: The three principal mounts used in this study. Mounts are A) robin in wing droop mobbing display, B) stoat model with robin in its mouth, C) blackbird in mobbing posture. Mounts are more fully described in Chapter 3.

I recorded robin "rapid alarm" calls (equivalent to "fast loud chucks" of Hay 1975, p.18) from a male on Allports Island in September 1989, using a Uher (Report 4000L) reel-to-reel tape recorder, microphone and parabola. The rapid alarm call was possibly given in response to a weka seen nearby, but this call is apparently used very generally in response to threatening stimuli, including harrier hawks, *Circus approximans*, weka, predatory mammals, people and possibly conspecifics (Flack 1979, Hay 1975, Powlesland 1980, pers. obs.). I recorded robin distress calls (Hay 1975, p.26) into a hand-held cassette recorder (Sanyo model M1001A) from a near-independent juvenile on Motuara Island in October 1990. Blackbird alarm calls were recorded by S.L. Dean at Kowhai Bush in 1988.

All tapes were edited to provide a continuous sequence of calls 5 mins in length.

Training regimes used

One of five training regimes was randomly assigned to each pair after their nest was found. The layout of mounts in the training arena and description of each of the five training regimes are described in Fig 3.1 and Table 3.1. Regime designs were based on preliminary training attempts on Allports Island (Chapter 1). Robins in Regime ROBMOB experienced "full training", ie. both audible and visual mobbing stimuli. Regime BKBMOB (blackbird and blackbird alarm call) was a control for any situation where a bird mobs a stoat with alarm calls. Regime ALARM was a control for the response of robins to an audible alarm stimuli without visual cues provided by the mobbing robin mount. In Regime DISTRES the focus was shifted away from a mobbing event and onto a robin in distress held in the stoats mouth, and Regime NOTRAIN measured the baseline response of untrained robins towards the stoat placed 1-1.5m from the nest.

Comparisons

Nest-defence responses of robins were compared using both the overall intensity score (Table 1.2) and the individual behaviours, times and distance measures (Table 1.1).

Table 3.1: Description of the training regimes used and the stimulus presented at the nest on Day 3.

Bird Mount	Enemy Stimulus	Calls Played Through Speaker	Enemy Stimulus Presented on Day 3
Regime			
ROBMOB			
Robin in mobbing posture	Stoat with dead robin in mouth	Robin alarm	Stoat
BKBMOB			
Blackbird in mobbing posture	Stoat with dead robin in mouth	Blackbird alarm	Stoat
ALARM			
None	Stoat with dead robin in mouth	Robin alarm	Stoat
DISTRES			
None	Stoat with dead robin in mouth	Robin distress	Stoat
NOTRAIN			
None	None	None	Stoat

Comparisons were made:

1) between training regimes, in the response of female robins towards the stoat at the nest on Day 3;

2) within training regimes, in differences in response between sexes during each training event on Day 2;

3) between training regimes, in the average response given by robins towards the stoat during each training event on Day 2, and;

4) between the response given during the training event on Day 2 and the response

of the female of the same pair during the stoat presentation on Day 3.

Analyses

Overall intensity score and individual body movement behaviours (wing flicks, flights and hops), times and distances were compared between training regimes using Kruskal-Wallis tests. If this overall comparison was significant (at $p<0.05$), planned comparisons were made between all possible pairs of regimes using Wilcoxon Sign Rank tests. For these pair-wise comparisons a conservative critical p-value of 0.01 was used because of the large number of comparisons made. Where a datum was missing the pair of data points were dropped from the analyses.

Because of very low and similar rates of alarm-calling given by male and female robins in each training event and by female robins on Day 3, this behaviour was not analysed. For the same reason other uncommon feather and displacement displays (bill-wiping, wing-drooping, raising head feathers or frontal spot) were pooled into a single category, "body displays" within each regime. Comparisons of body displays between training regimes were made using Chi-square tests.

The behaviours, times and distance categories given at training events on Day 2 were compared with the response intensity scores of female robins given towards the stoat on Day 3 using Spearman Rank Correlations, with a critical p-value of 0.05.

RESULTS

A total of 100 pairs of incubating robins were used for training experiments, with nests divided evenly between the five training regimes. Twenty two tests were completed in 1989 and the remainder were completed in 1990.

Comparison of nest-defence responses of females among training regimes one day after training

Results of statistical tests are presented in Table 3.2. The intensity of nest-defence by females varied significantly among training regimes (Fig 3.3).

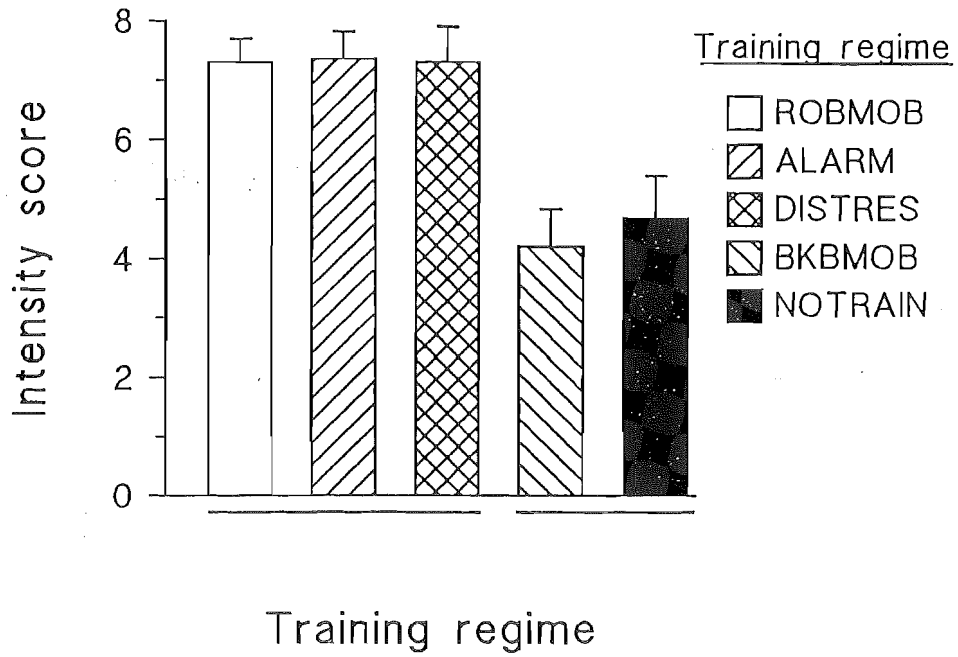


Figure 3.3: Mean (±se) response intensity score per trial by robins presented with the stoat at their nests one day after being trained, using regimes ROBMOB, ALARM, DISTRES, BKBMOB and NOTRAIN (N=20 per regime). The line under the x-axis at an equivalent level indicates pairwise comparisons that are not significantly different from each other at $p<0.01$.

Table 3.2: Differences among training regimes in response of robins to stoat presented outside the nest the day after training. Pair-wise comparisons were between NOTRAIN (N), ROBMOB (R), DISTRES (D), ALARM (A) and BKBMOB (B) training regimes.

Variable Measured	Training Regime KW value#	p-value	Significant Pairwise Comparisons##
Flights	18.66	<0.001	R=A=D>B
Wing flicks	20.03	<0.001	R=A>N=B
Hops	16.82	0.002	R=A>N=B
Closest approach	9.44	0.051	R>B
Time in view of the stoat	17.20	0.002	A>N=B
Total time off during test	NS		
Time off after seeing stoat	11.41	0.022	NS
Time on nest post trial	NS		
Time off nest post trial	NS		
Body displays+			
X^2	df	p	Difference
10.2	4	0.037	R=D>B=N

= Kruskal Wallis tests between training regimes
= Wilcoxon Sign Rank tests for pairwise comparisons, p<0.01
+ = Chi-square test

Female robins trained using regimes involving conspecific mounts and calls (ROBMOB, ALARM and DISTRES) responded at a significantly higher intensity to the stoat near the nest than did untrained robins (NOTRAIN), or females trained without robin mounts and calls (BKBMOB). Thus, training using conspecific mounts and calls had a positive influence on the subsequent recognition test conducted 24 hrs later.

When nest-defence responses of females towards the stoat were analysed separately, there were significant differences among the training regimes in most of the behaviours, times and distances measured, with ROBMOB, ALARM and DISTRES trained females responding to the stoat at a comparatively higher level than females trained with BKBMOB, or NOTRAIN

Specifically, the number of body movements, the amount of time spent in view of the stoat (Fig 3.5), the time away from the nest after sighting the stoat (Fig 3.6), and the number of trials in which body displays were given (Fig 3.7) all varied significantly among regimes. Planned pairwise comparisons indicated that ROBMOB and ALARM trained females gave significantly more body movements towards the stoat than did BKBMOB trained females, and DISTRES trained robins gave significantly more flights than BKBMOB trained females.

Body displays were recorded in significantly more stoat presentations to females that had been trained using DISTRES and ROBMOB regimes than to BKBMOB and NOTRAIN trained females.

There were no differences among regimes in the total time the female stayed off the nest during tests where a stoat was presented at the nest (Fig 3.6), in the natural times females spent on or off the nest prior to training, in the length of time spent on or off the nest immediately after the stoat was removed (Fig 3.8).

Although the overall average closest approach distance to the stoat did not vary significantly among regimes ($p=0.051$), females trained using ROBMOB approached the stoat significantly closer than did BKBMOB trained females ($p<0.01$, Fig 3.9). In most of the non-significant results the trend was the same as for the significant comparisons, with females responding more strongly towards the stoat if they had been trained using regimes incorporating robin mounts and calls than if untrained or trained using mounts and calls from a different species.

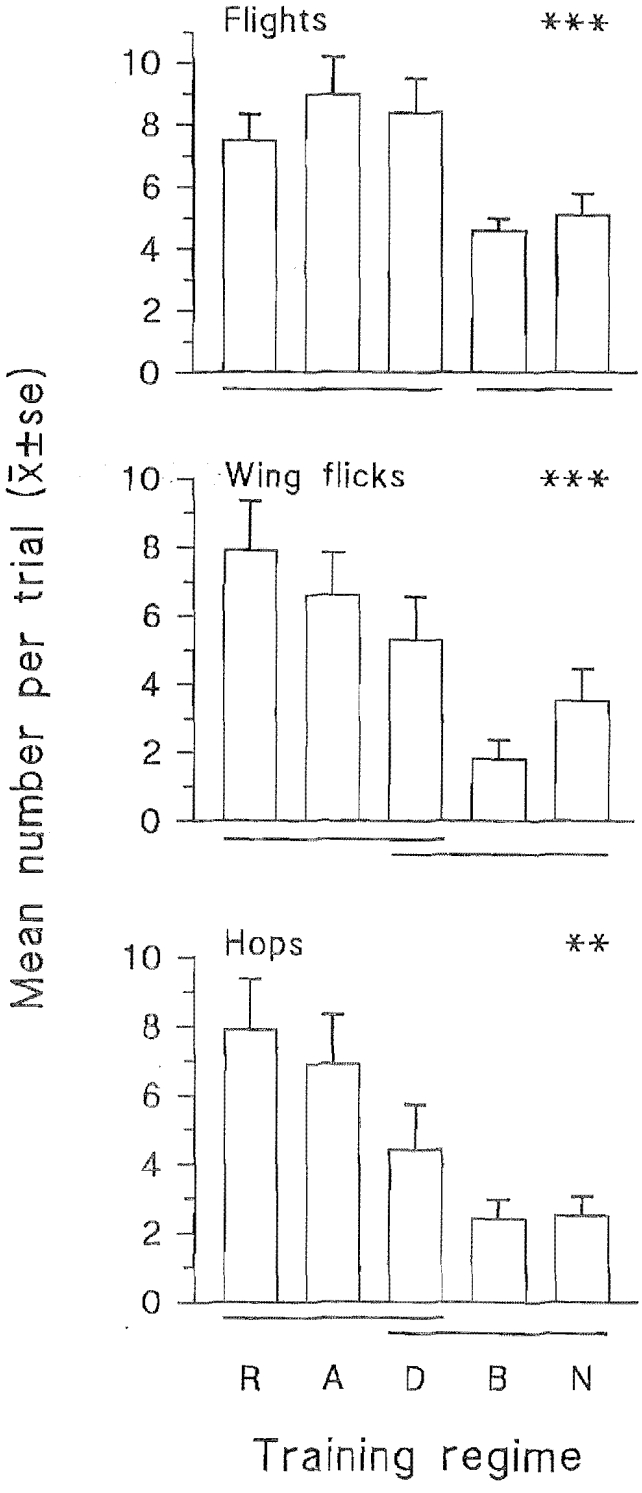


Figure 3.4: Mean (±se) number of flights, wing flicks and hops per trial by robins presented with the stoat at their nests one day after being trained (N=20 per regime). Training regimes are ROBMOB (R), ALARM (A), DISTRES (D), BKBMOB (B) and NOTRAIN (N) and are fully described in Chapter 3 and Table 3.1. The lines under the x-axis at an equivalent level indicate pairwise comparisons that are not significantly different from each other at $p<0.01$. ** shows $p<0.01$, *** $p<0.001$, for the comparison among all regimes.

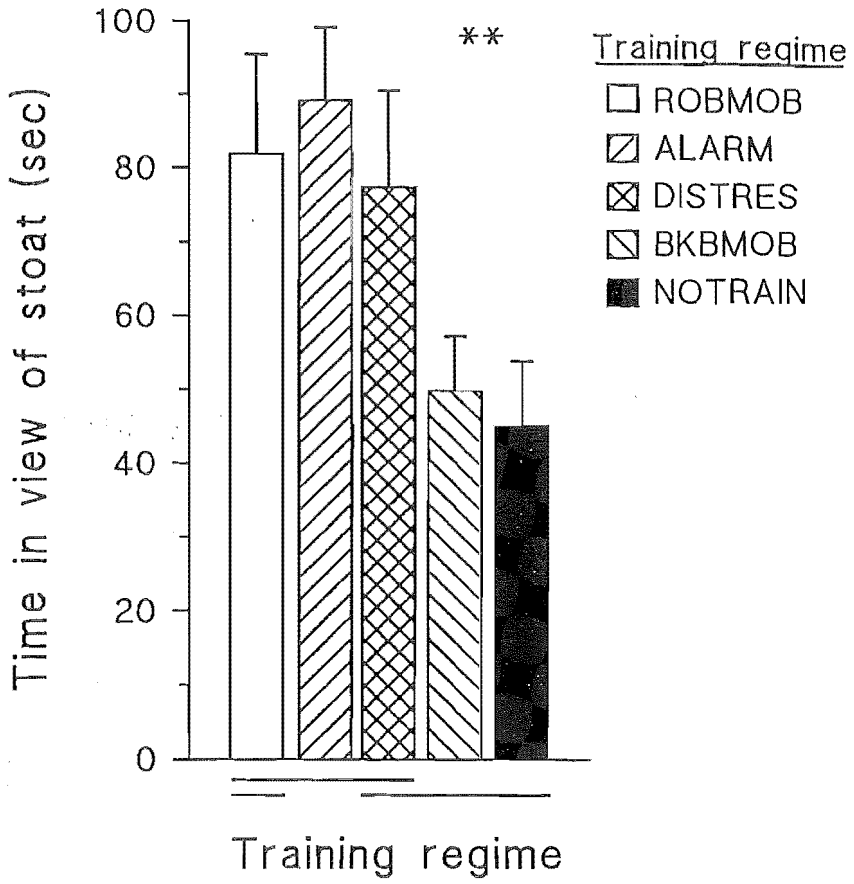


Figure 3.5: Mean (±se) time in view of the stoat per trial by robins presented with the stoat at their nests one day after being trained (N=20 per regime). Training regimes are fully described in Chapter 3 and Table 3.1. The lines under the x-axis at an equivalent level indicate pairwise comparisons that are not significantly different from each other at $p<0.01$. ** shows $p<0.01$, for the comparison among all regimes.

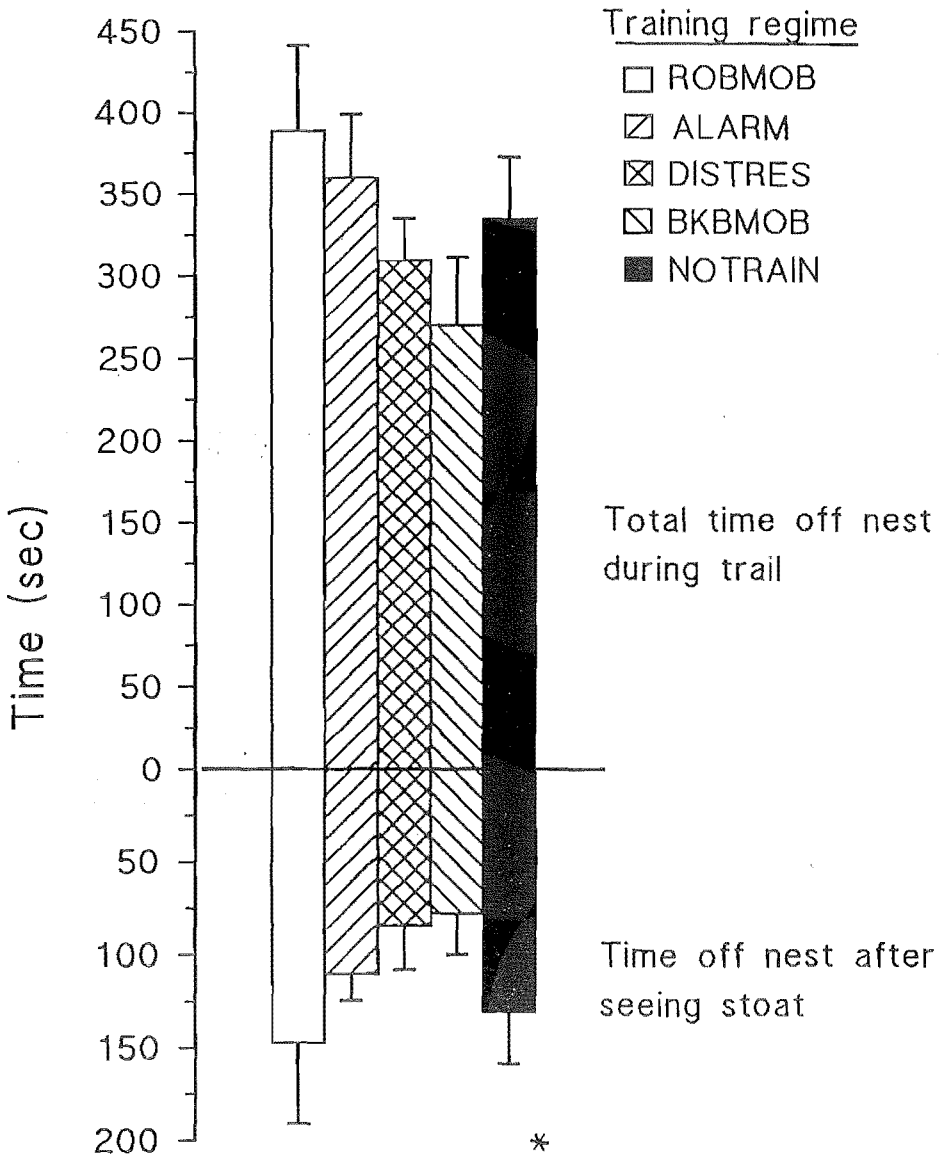


Figure 3.6: Mean (±se) total time off the nest and total time off the nest after seeing the stoat for trials where robins were presented with the stoat at their nests one day after being trained (N=20 per regime). Training regimes are fully described in Chapter 3 and Table 3.1.

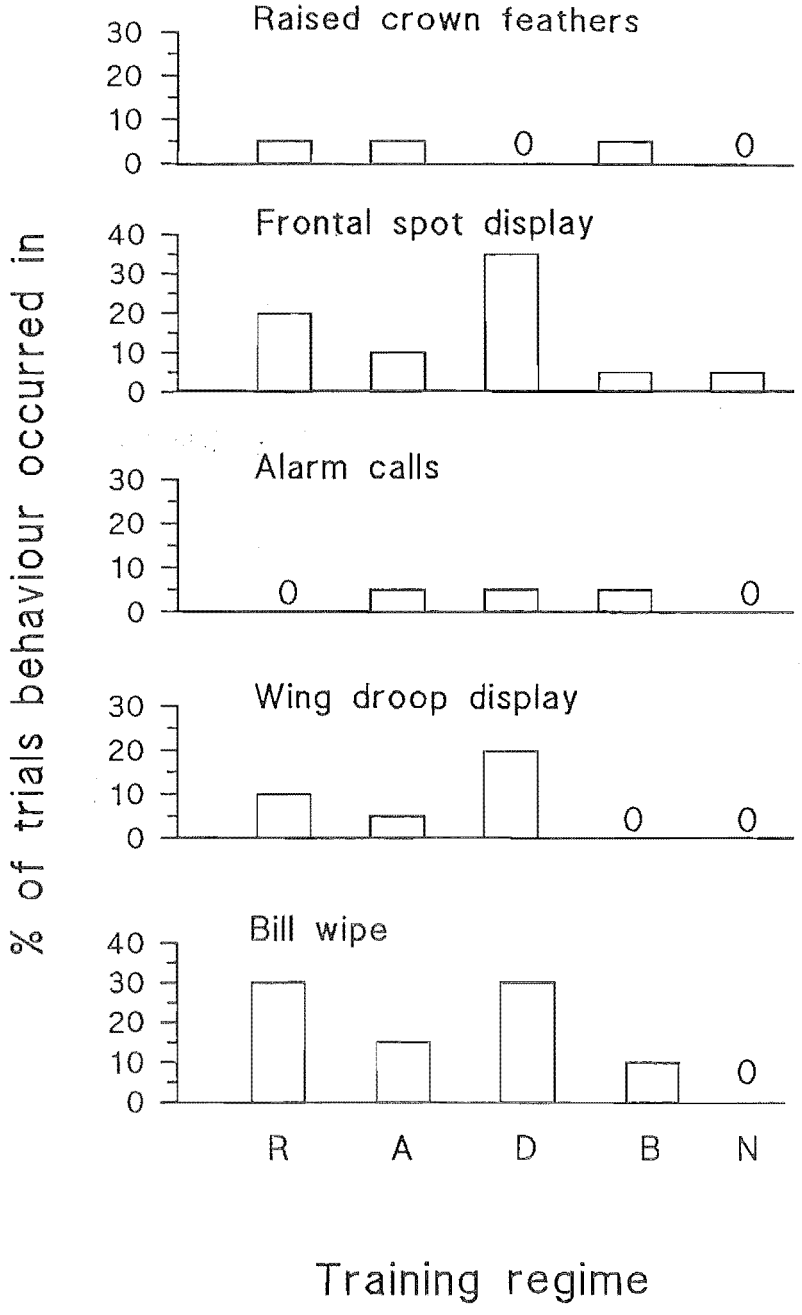


Figure 3.7: Frequency of trials in which robins gave body displays or alarm called when presented with the stoat at their nests one day after being trained (N=20 per regime). Training regimes are ROBMOB (R), ALARM (A), DISTRES (D), BKBMOB (B) and NOTRAIN (N) and are fully described in Chapter 3 and Table 3.1.

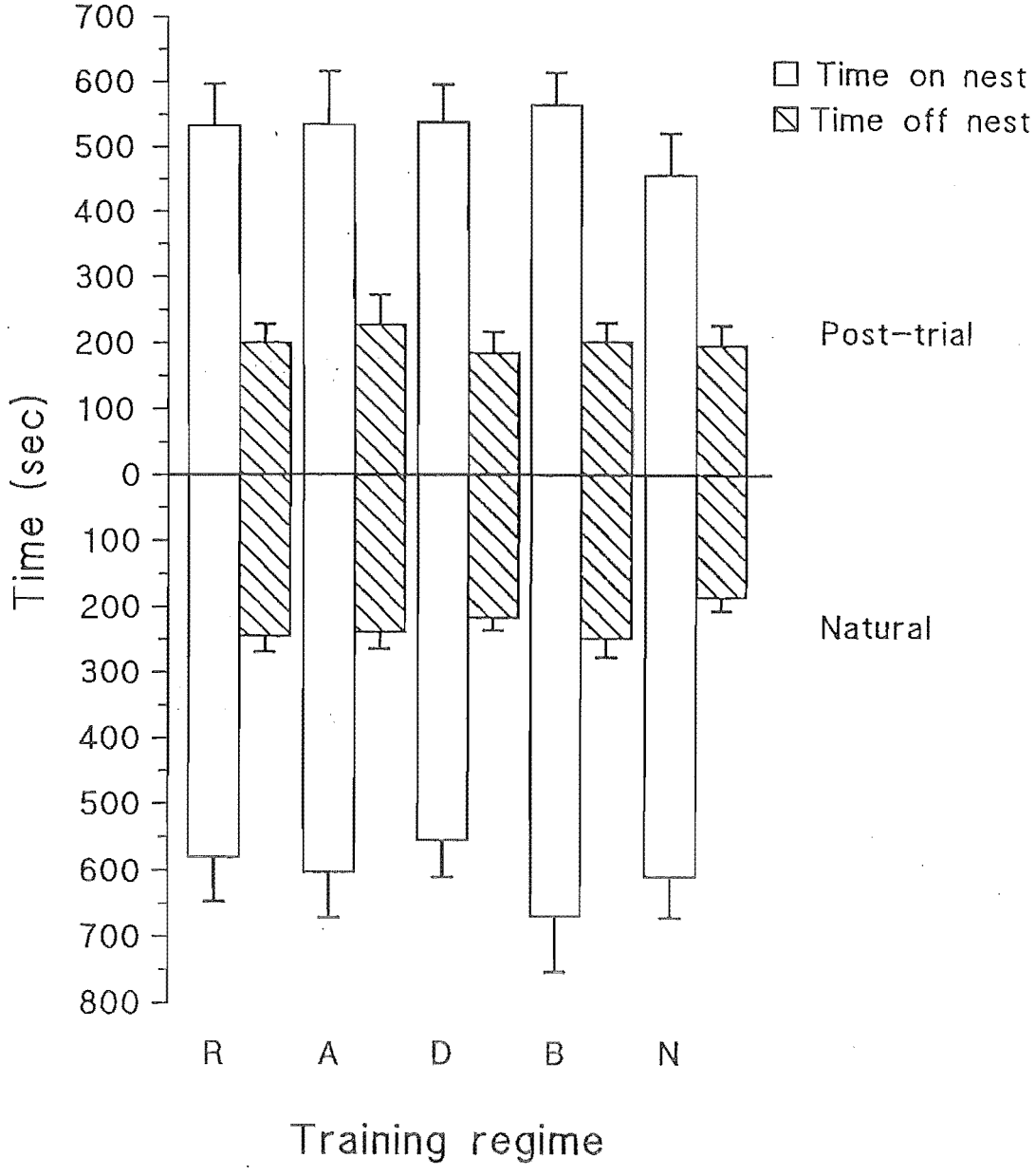


Figure 3.8: Mean (±se) time on and off the nest before (natural) and immediately after (post-trial) the stoat presentation, for trials where robins were presented with the stoat at their nests one day after being trained (N=20 per regime). Training regimes are ROBMOB (R), ALARM (A), DISTRES (D), BKBMOB (B) and NOTRAIN (N) and are fully described in Chapter 3 and Table 3.1.

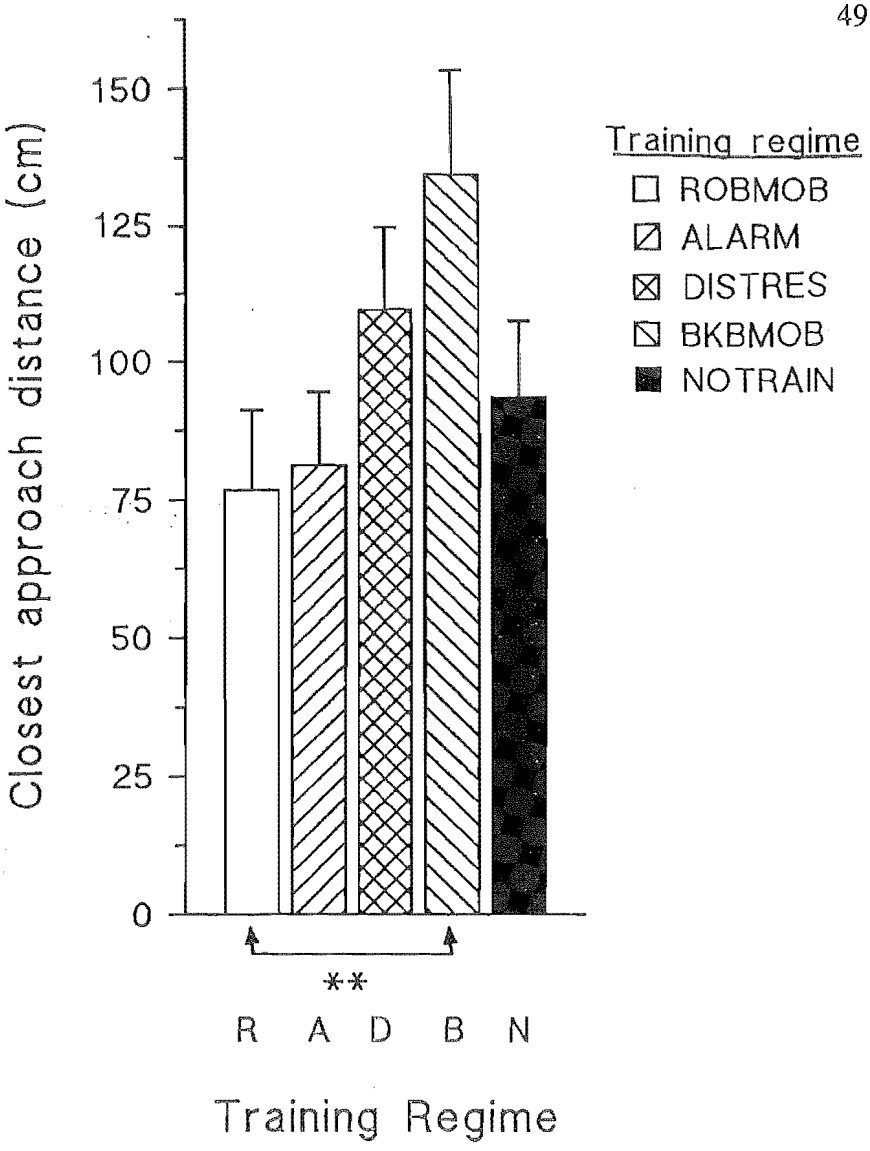


Figure 3.9: Mean (±se) closest approach distance by robins to the stoat, for trials where robins were presented with the stoat at their nests one day after being trained (N=20 per regime). Training regimes are ROBMOB (R), ALARM (A), DISTRES (D), BKBMOB (B) and NOTRAIN (N) and are fully described in Chapter 3 and Table 3.1. ** shows $p<0.01$ for the pairwise comparison arrowed.

Differences between responses of male and female robins during training

Results of statistical tests are presented in Table 3.3. Females were present for all 80 training events, and males were present for 77 training events (absent from one ALARM, DISTRES and BKBMOB event).

There were significant differences between the sexes in average number of wing flicks during training using ROBMOB, ALARM and BKBMOB regimes, and in number of hops during the ALARM regime; with females responding more strongly than males (Fig 3.10). Females were more likely than males to alarm call and bill-wipe, whereas males raised their head feathers, wing-drooped and displayed their frontal spots in more training events than females, although none of these differences were significant (Fig 3.11).

There were no significant differences between the sexes in any regime in average number of flights during training event (Fig 3.10), in the closest approach distance to the training mounts (Fig 3.12) or in time in view of the training arena (Fig 3.13).

Table 3.3: Statistical results for differences in response of male and female robins during training events.

Variable Measured#	p-value for each training regime ROBMOB	BKBMOB	ALARM	DISTRES
Flights	NS	NS	NS	NS
Wing flicks	0.002	0.002	0.001	NS
Hops	NS	NS	0.02	NS
Closest approach	NS	NS	NS	NS
Time in view of training arena	NS	NS	NS	NS
Body displays+				
X^2	df	p	Difference	
0.86	3	0.835	NS	

\# = Wilcoxon Sign Rank tests
\+ = Chi-square test

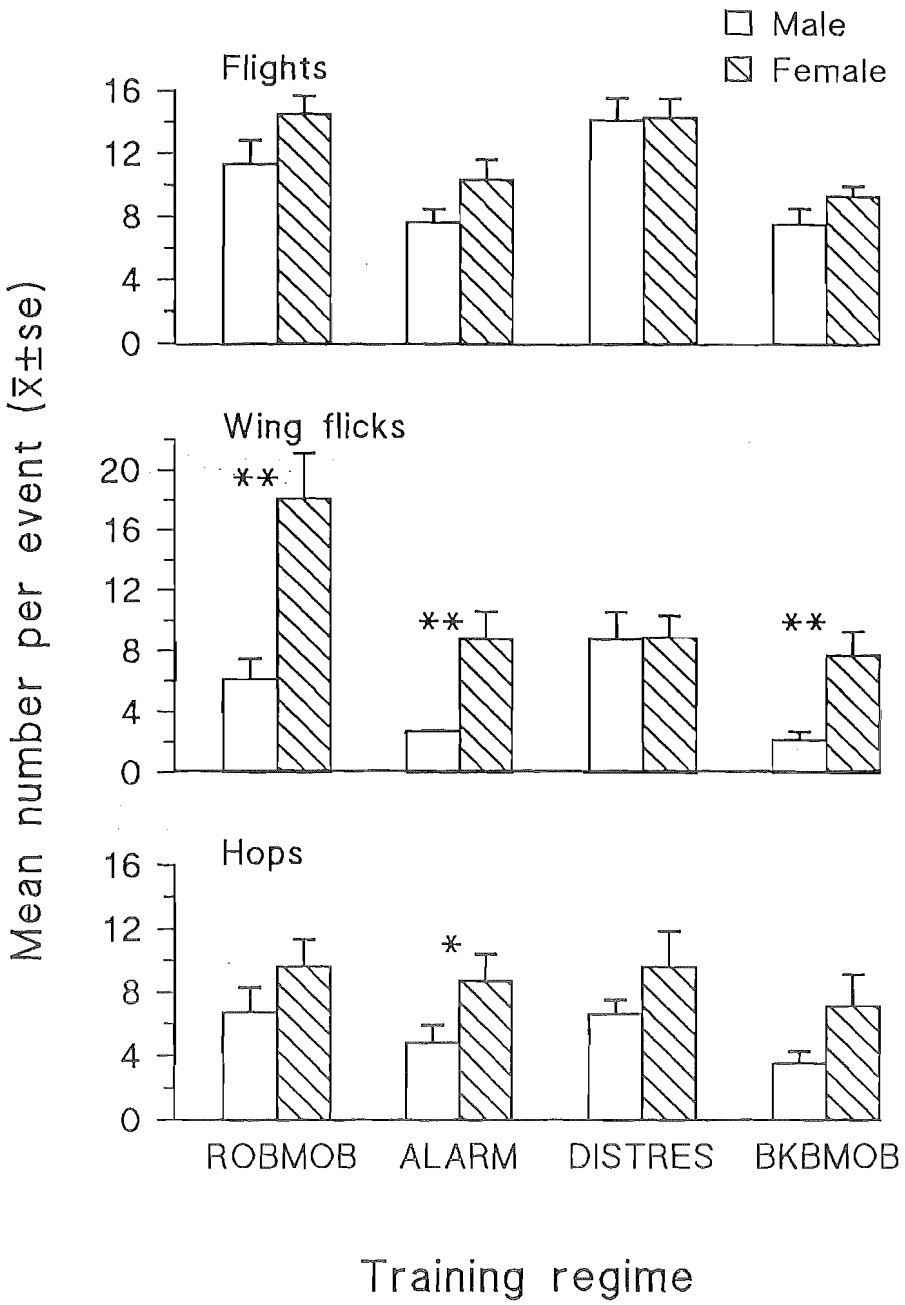


Figure 3.10: Mean (±se) number of flights, wing flicks and hops per trial by robins during training (N=20 per regime). Training regimes are fully described in Chapter 3 and Table 3.1. * shows $p<0.05$, ** shows $p<0.01$, for comparisons between males and females.

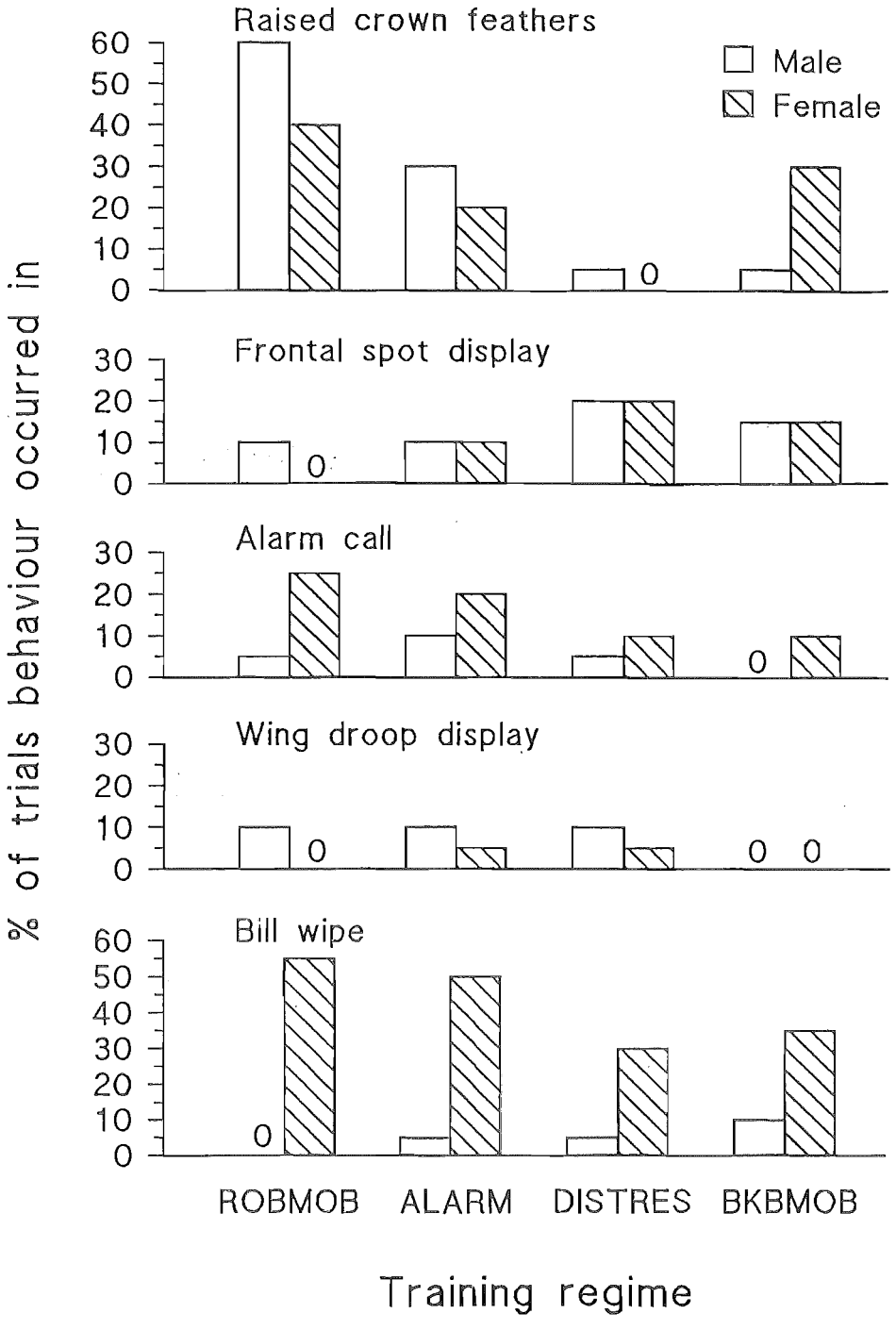


Figure 3.11: Frequency of trials in which male and female robins gave body displays or alarm called during training (N=20 per regime). Training regimes are fully described in Chapter 3 and Table 3.1.

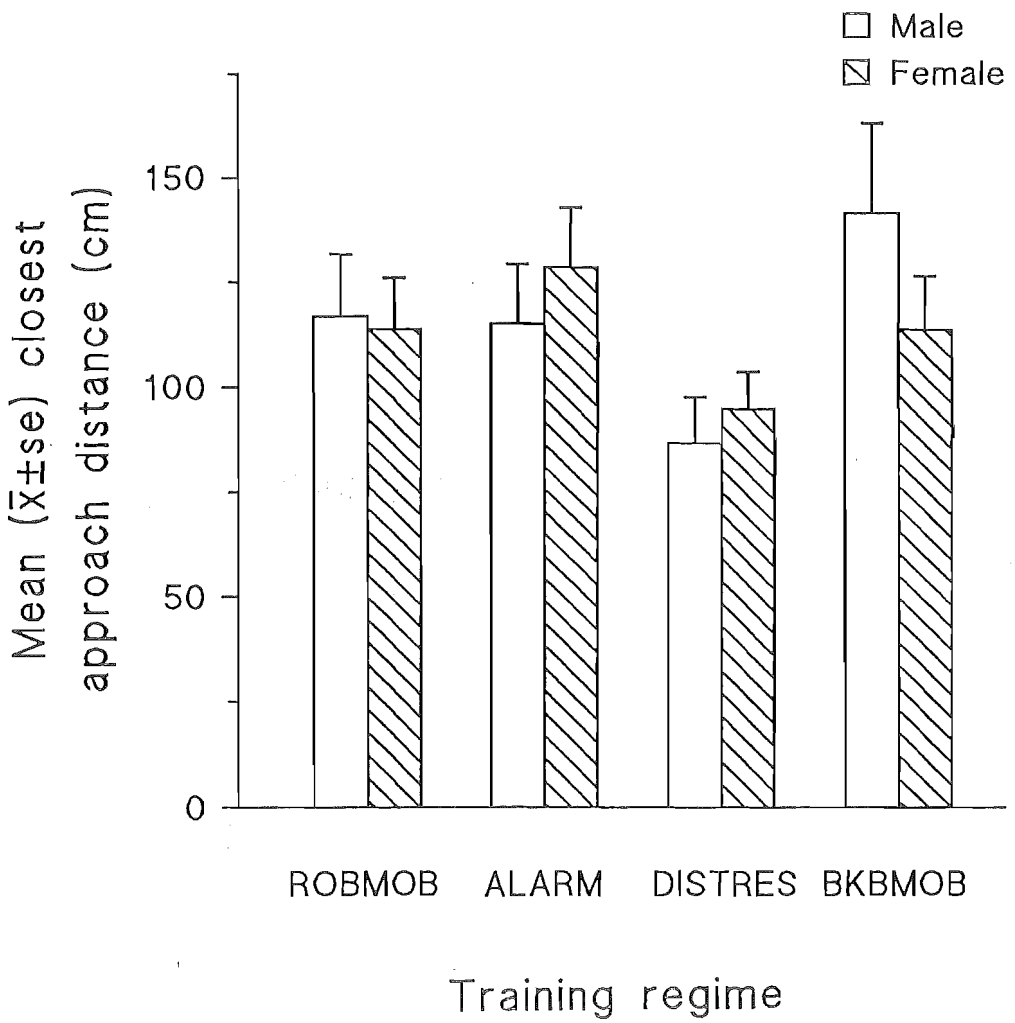


Figure 3.12: Mean (±se) closest approach distance per trial of male and female robins to the stoat during training (N=20 per regime). Training regimes are fully described in Chapter 3 and Table 3.1.

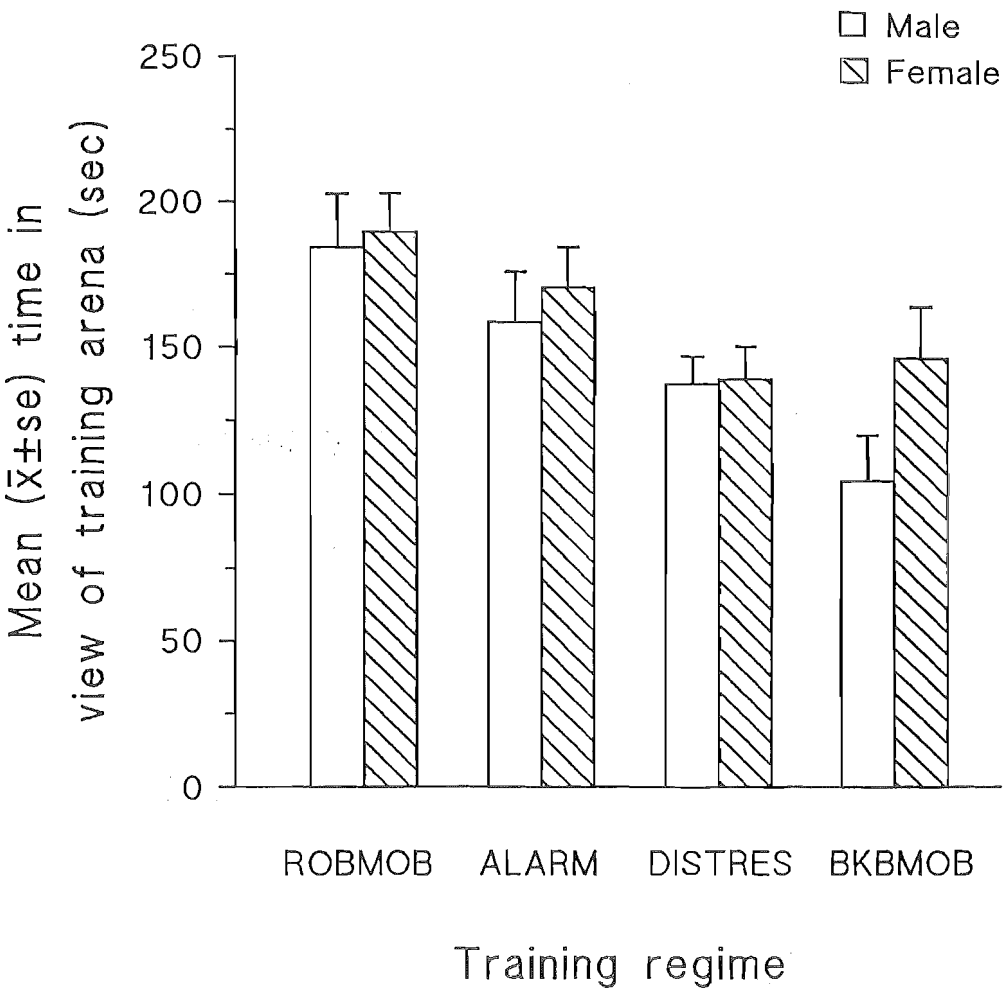


Figure 3.13: Mean (±se) time in view of the stoat per trial, of male and female robins during training (N=20 per regime). Training regimes are fully described in Chapter 3 and Table 3.1.

Differences in responses of robins between training regimes during training

Results of statistical tests between regimes are presented in Table 3.4. The average of male and female responses were used in comparisons between training regimes.

Table 3.4: Differences among training regimes during training using the average male and female response values. Pair-wise comparisons were between ROBMOB (R), DISTRES (D), ALARM (A) and BKBMOB (B) training regimes.

Variable Measured	KW value#	Training Regime p-value	Significant Pair-wise## Comparisons
Flights	21.31	<0.001	R=D>A=B
Wing flicks	13.70	0.003	R>A=D=B
Hops	7.64	NS	
Closest approach	5.07	NS	
Time in view of training arena	6.00	NS	
Body displays+			
X^2	df	p	Difference
3.73	3	0.293	NS

= Kruskal-Wallis tests between all training regimes, $p<0.05$
= Wilcoxon Sign Rank tests of pairwise comparisons, $p<0.01$
\+ = Chi-square test

There were significant differences between the regimes in the number of flights (ROBMOB=DISTRES>ALARM=BKBMOB) and wing flicks (ROBMOB> ALARM=DISTRES=BKBMOB, Fig 3.14).

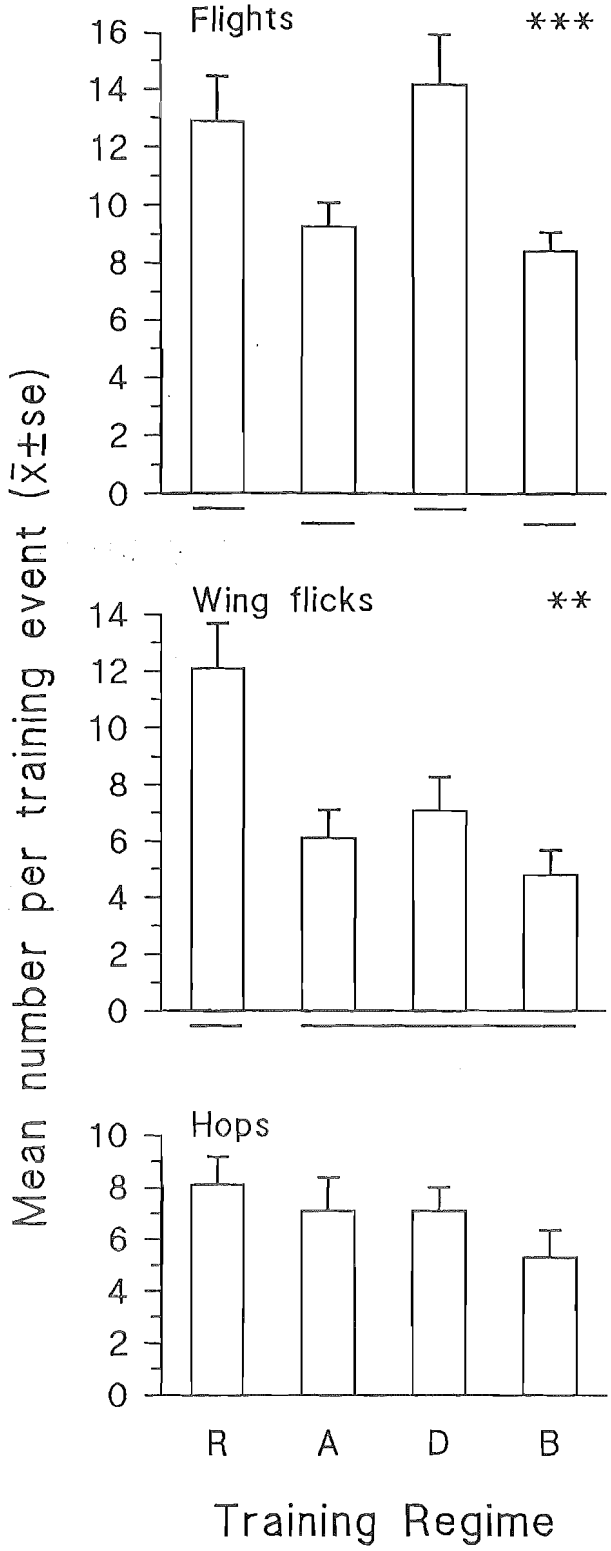


Figure 3.14: Mean (±se) number of flights, wing flicks and hops per trial by robins during training (N=20 per regime). Bars are means of male and female responses within a pair. Training regimes are ROBMOB (R), ALARM (A), DISTRES (D), BKBMOB (B) and NOTRAIN (N) and are fully described in Chapter 3 and Table 3.1. The lines under the x-axis at an equivalent level indicate pairwise comparisons that are not significantly different from each other at $p<0.01$. ** shows $p<0.01$, *** $p<0.001$, for the comparison between all regimes.

The average time spent in view of the training arena during training (Fig 3.15a), the average closest approach distance to the mounts (Fig 3.15b) and the rates of body displays (Fig 3.16) were not significantly different among training regimes during training.

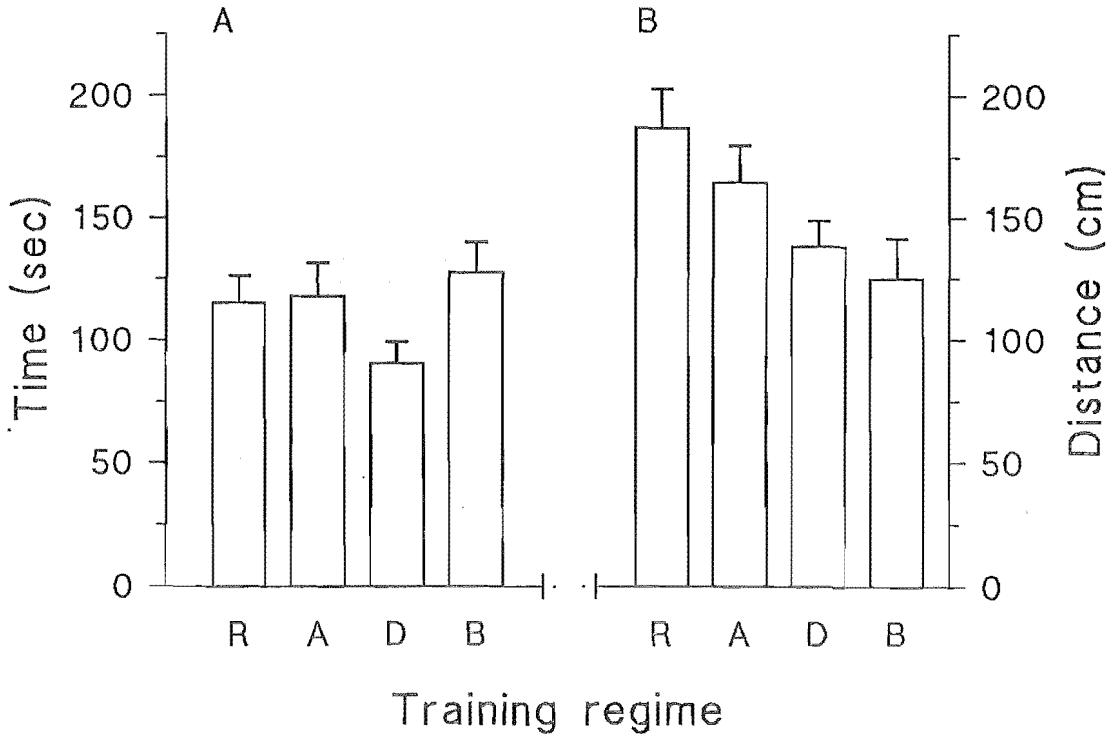


Figure 3.15: Mean (±se) time in view (A) and mean (±se) distance (B) from the stoat by robins during training (N=20 per regime). Bars are means of male and female responses within a pair. Training regimes are fully described in Chapter 3 and Table 3.1.

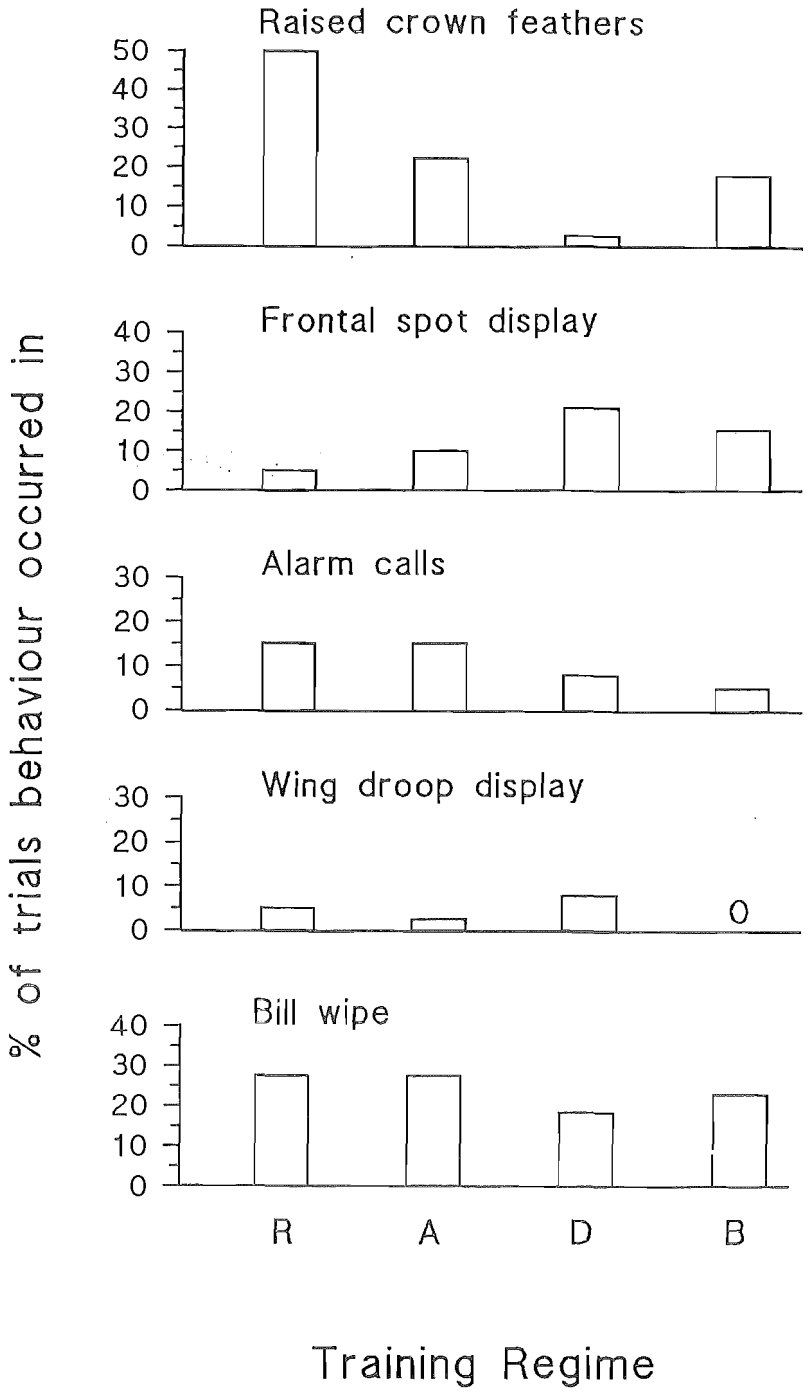


Figure 3.16: Frequency of trials in which robins gave body displays or alarm called during training (N=20 per regime). Bars are means of male and female responses within a pair. Training regimes are ROBMOB (R), ALARM (A), DISTRES (D), BKBMOB (B) and NOTRAIN (N) and are fully described in Chapter 3 and Table 3.1.

Relationship between the response of robins during training and the response of females one day after training

Correlation coefficients for comparisons between the average of male and female behaviours during training (Day 2) with the females response towards the stoat (Day 3) are given in Table 3.5.

No behaviours, times or distance measures of robin behaviour during training on Day 2 was significantly correlated with the response intensity score of females on Day 3. Generally, higher intensity responses on Day 3 were given by robins that flew more and wing flicked less during BKBMOB training, by robins that wing flicked more and stayed in view of the training arena longer during ALARM training, and by robins that wing flicked more during DISTRES training.

Table 3.5: Correlation coefficients for the response of robins during training events with response of females one day after training.

Variable Measured	r-value for each training regime			
	ROBMOB	BKBMOB	ALARM	DISTRES
Flights	0.019	0.269	0.102	-0.152
Wing flicks	0.108	-0.314	0.294	0.310
Hops	0.132	-0.059	-0.131	-0.201
Closest approach	0.176	-0.080	-0.002	0.047
Time in view of stoat	-0.044	0.082	0.321	0.071
Sample Size	20	19	18	19
Critical r-value for $p<0.05$	0.444	0.389	0.378	0.389

DISCUSSION

Comparison of nest-defence responses of females between training regimes one day after training

Clearly, robins on Motuara Island can learn to recognise an enemy after only one previous interaction with that enemy. Robins who were trained to recognise an enemy stimulus as a threat responded in a future encounter with that enemy near the nest by giving more intense nest-defence responses than untrained robins or robins trained with the blackbird mount and calls.

Learning of nest-defence responses required experience with *conspecific* mounts and calls; robins who were trained with the blackbird mount and calls did not respond differently from untrained robins. There were differences in the type and intensity of response given towards the stoat after training and this was dependent on the conspecific training regime used.

Training was effective with and without the presence of the mobbing robin mount, but most of the nest-defence response behaviours were given at a higher rate if the mobbing robin mount was included in the training regime design. Robins trained using distress calls and robins trained with conspecific mounts plus robin alarm calls frequently gave body displays to the stoat. However, unlike the other conspecific training techniques, robins trained using distress calls responded at an intermediate level in all other behaviour, time and distance measures. Robins trained with robin alarm calls responded by giving more of all behaviours and times measured than did untrained robins, but only gave body displays at a level intermediate to distress call trained and untrained robins.

In this study, the experimental design only tested for retention of the training experience over one night. It is not known whether enhanced responses can be retained for periods greater than 24 hours, nor how long the increased nest-defence response would continue in the absence of further experience with the enemy.

Although responses towards the stoat of robins trained using conspecific mounts were significantly greater than responses of untrained robins, the responses were noticeably less than those given by robins with chicks towards the stoat in Kowhai Bush (see Chapter 2), particularly with respect to high intensity nest-defence

behaviours such as body displays and alarm calling.

Enhancement of nest-defence responses of robins using the artificial training technique was remarkably successful, and future experiments should focus on developing the *best* training regime design. I suggest that the training regime must involve three things to be effective as a teaching method. First, the training regime must keep the attention of the trainees for as long as possible. Second, the regime should reflect real-life situations so that the trainees are likely to associate the regime with realistic enemy encounters, and third, the training event should be effectively focused on the object of training (ie. on the enemy stimulus). This can be achieved by using a moving enemy stimulus, or by leaving out other parts of the regime which may serve as distractions. For example, in my study, the robin mount may have distracted the attention of the strongly territorial test pair.

Possible alterations to the methodological detail of the training design that I used could include: 1) an increase in the number of training events; 2) a decrease in the length of each training event, and 3) a planned variation in length and training regime type (eg. using alarm and distress calls). By incorporating some or all of these refinements into future training experiments researchers may reinforce the desired response to the enemy stimulus, but at the same time avoid habituation. A shorter training event than the 5 min used in this study may be adequate; robins rarely stayed in the training arena for the full 5 min period.

Differences in responses of male and female robins during training

Although females gave relatively more low intensity responses (wing-flicks and hops) during training events, I suggest that male and female robins respond to an enemy within their territory at behaviourally similar levels. Wing flicks and hops may not reflect differences in motivational state or in assessment of risk of injury from the enemy (see McLean & Rhodes 1991). If either bird was motivated to respond strongly this should be reflected in the number of high intensity nest-defence behaviours (ie. body displays, alarm calls) given to the stoat. However, high intensity responses were rarely and equally given by each sex in all training regimes.

Differences in response of robins between training regimes during training

Robin response during training was dependent on the type of training given. Response was always highest for training regimes using robin mounts, alarm calls and robin distress calls and lowest in training involving another species. I suggest these differences in response are due to differences in natural reactions of robins to mobbing events. Robins do not commonly join mixed-species mobbing flocks (Dean 1989) and so it may not be surprising that robins responded weakly towards a training event depicting a blackbird mobbing an unknown enemy. In comparison, robins are attracted to calls of conspecific (Hay 1975).

It is possible that responses during the ROBMOB training regime were high because robins were reacting to the presence of a strange conspecific in their territory. However, when robins approached the training arena they appeared to be responding to the stoat, and on no occasion did robins ever attack the "intruding" robin mount.

Relationship between the response of robins during training and the response of females one day after training

These results indicate that no variable recorded during training was significantly correlated with the intensity of response given the day after training.

Identification of a behaviour given during training that correlates well with future response intensity could increase trainer confidence that the birds have been trained adequately. For example, training could continue until the "indicator" behaviour was recorded at a predetermined level, indicating that future response to the enemy is likely to be strong.

CHAPTER 4

Cultural transmission of nest-defence behaviours between generations

Anti-predator defence behaviours such as nest-defence in birds may be transferred between generations by genetic or cultural transmission (eg. Conover 1987, Curio 1975, Findlay 1991, Klopfer 1957, Mueller & Parker 1980, and see Chapter 1). Cultural transmission of predator-information is where birds learn to recognise and respond to a predator by watching the behaviour of other individuals, either conspecifics or other species (equivalent to "traditional transmission" of Temple 1977a). The ability to obtain information by cultural transmission may be an effective means of acquiring skills without a high risk of injury (Alder 1975, Temple 1977b, Vieth *et al.* 1980).

The opportunity to witness others mobbing a predator may occur frequently, especially for members of a colonial species or for offspring that have a close association with parents (Kruuk 1976, Shields 1984). However, evidence that birds have the opportunity to learn how to recognise and respond to predators does not provide support for cultural transmission *per se*; stronger support comes from studies showing that birds actually learn *and* use information about predators that is gained from watching others.

Cultural transmission of the ability to learn avoidance responses or to learn to recognise and respond to predators has been demonstrated on at least four occasions. Klopfer (1957) showed that ducks learned to avoid a feeding dish ("predator") where they had observed other ducks receiving electric shocks. Furthermore, the ducks who were not trained to avoid the dish, but who had witnessed training of the first group of ducks, were able to transmit the avoidance behaviour to a third group of ducks. In the laboratory, Vieth *et al.* (1980) were able to pass mobbing behaviours from experienced to naive blackbirds, *Turdus merula*, through six individuals with no loss of mobbing potency. They were also able to teach blackbirds to mob a non-predatory object by providing a naive student blackbird with the impression that an experienced tutor bird was mobbing the object (Curio *et al.* 1978a, 1978b). Alder (1975) showed that a subspecies of vole,

Clethrionomys glareolus, living in a predator-free area was more docile (≡ less fearful?) when handled than a similar sub-species in an area with predators. By cross-fostering young of the docile sub-species to the more active (≡ more fearful?) voles, Alder found that the previously docile young became behaviourally indistinguishable from the active voles. Finally, Conover (1987) showed that ring-billed gulls, *Larus delawarensis*, who were passive mobbers (ie. flew quietly on the outer edge of a predator-gull mobbing event), gained information about the predator and learned appropriate mobbing responses.

Cultural transmission of nest-defence behaviours *between generations* may occur when near-independent fledglings witness their parents' response to a predator by the nest. Hirsch & Bolles (1980, p.72) consider this unlikely, as there will be a "...low probability of a second prey animal [eg. a fledgling] being witness to an act of predation." However, in many species, fledglings remain with the parent(s) for a long pre-independence period and there is sufficient time to witness and learn from parent-predator interactions (also see parallel studies on song-learning in birds, eg. Gyger *et al.* 1986, Marler & Peters 1977, Marler & Tamura 1964).

Because of the lessened risk of injury if fledglings learn to recognise and respond to predators through cultural transmission (Bolles 1970), predator-naive birds may use this method rather than the alternative of confronting the predator and learning by trial and error. However, no field study has shown that predator-naive juvenile birds incorporate nest-defence behaviours into their behavioural repertoire after witnessing the response of another individual towards a predator.

If cultural transmission of nest-defence behaviours is an important means of acquiring defence skills in juvenile birds, then I predict that fledglings should be receptive to artificial training to enhance such defence skills.

The aim of this chapter is to test the hypothesis that nest-defence behaviours may be passed between generations by cultural transmission. Specifically, I compare the nest-defence responses of adult robins who, as fledglings, witnessed an artificial training event between their parent(s) and a predator, the stoat.

METHODS

General methods

Fledgling robins with known parents were trained on Motuara Island in 1989. All birds were individually colour banded either in the nest before training or within a few days after training. Parents at 20 nests used in this experiment were previously used in other stoat recognition and response experiments (15 in Chapter 2 enemy recognition experiments and five in Chapter 3 training experiments). The previous experience of the parents with the stoat, or training regimes, and a list of band combinations of trained fledglings and parents are given in Appendix 3.

Training procedure

Initially I attempted to train fledgling robins while they were still in the nest, but the standard response to training was to freeze and lie low in the nest, out of view of the training stimulus. Therefore, I trained chicks after fledging but before independence, using training regime ROBMOB, described in Chapter 3. ROBMOB training involved a robin mount placed in a mobbing position and alarm calling at a predator (the stoat). Each fledgling received one 5 min training session, during which time they could observe both the training event and their parents' response towards the event. The responses of fledglings during training were recorded using the behaviours, times and distance variables described in Table 1.1.

Test procedure

The nest-defence responses of robins towards the stoat were tested one year after training by placing the stoat 1-1.5m from nests of robins during the egg stage (method described in Chapter 3). I recorded robin nest-defence responses towards the stoat using behaviour, time and distance categories described in Table 1.1.

Comparisons

There were four treatments which differed in the age and previous training experience of the robins. Two of the treatments involved known one year old robins who were either 1) TRAINED or 2) UNTRAINED as fledglings. The other

two treatments were included in the analyses because of the low sample sizes of TRAINED and UNTRAINED treatments. These treatments were 3) NOTRAIN and 4) ROBMOB regimes; both had sample sizes of 20 robins and were described and analysed in Chapter 3.

UNTRAINED robins were a subset of all yearling robins (n=2) from the NOTRAIN treatment, and the analysis of the NOTRAIN data included the two UNTRAINED robins. Of the training methods, the ROBMOB training regime was chosen as the fourth treatment as this regime had been used to train fledglings (shown the stoat one year after training) and adult females (shown the stoat one day after training). ROBMOB training had also resulted in the strongest learned nest-defence response for adults (Chapter 3).

Comparisons were made:

1) between TRAINED fledglings during training;

2) between TRAINED, UNTRAINED, NOTRAIN and ROBMOB robins, in behaviours, times and distance measures given towards the stoat presented at the nest.

Where appropriate, all data were analysed using Mann-Whitney U nonparametric statistical tests or Goodness of Fit tests.

RESULTS

A total of 29 fledglings from 26 nests were trained during the 1989 season.

Responses of fledglings during training

Throughout training, the responses of fledgling robins were fairly uniform. Fourteen (48%) of fledglings immediately froze on the spot in response to the training event. All of these birds remained in full view of the training arena for the 5 min (300 sec) training period, at an average distance of 3.4±0.37 m (range 1.5-7.0 m, Fig 4.1). The remaining 15 fledglings (52%) moved 1-11 times during training and therefore spent less time in view of the training arena (x=282 ± 33 sec). The average distance from the stoat during training was not significantly

different between fledglings that moved and those that remained motionless (U-test, p=0.21, closest approach distance for fledglings that moved during training was x=2.8 ± 0.25m, range 1.0-6.0m, Fig 4.1). No fledglings called or displayed during training, and all remained within probable hearing range of the training arena throughout the 5 min training period.

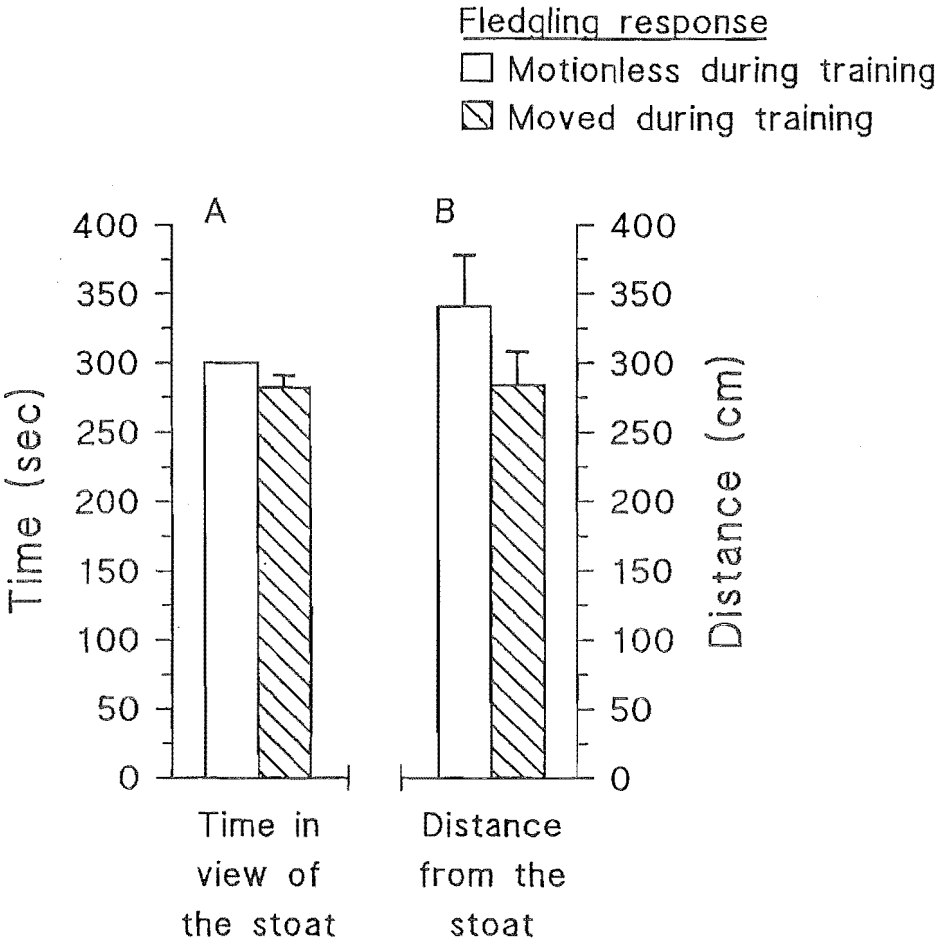


Figure 4.1: Mean (±se) time in view (A) and mean (±se) distance (B) from the stoat of fledgling robins during training (N=29). The training technique is fully described in Chapters 3 and 4.

Responses of robins to the stoat one year after training

Mortality rates of fledglings were very high between the 1989 and 1990 seasons. Only three (10%) fledglings TRAINED in 1989 were still alive on Motuara Island in 1990 (every robin on the island was found and identified in 1990). A higher proportion of banded and untrained fledglings survived between seasons (29%, 18/62), although the difference between the groups was not significant (Pearsons $X^2=2.58$, $p=0.11$).

Of the three surviving TRAINED robins, two were females who nested and were tested but the other was a non-breeding bachelor male who could not be tested. Two UNTRAINED robins were tested as one year old birds.

I did not statistically test differences between robin treatment types because of the small sample size. One of the two TRAINED females responded very strongly to the stoat, with body movements (hops, wing flicks and flights) at rates 5-15 times higher than UNTRAINED robins and twice as high as the maximum recorded movements for the 20 NOTRAIN robins (Fig 4.2). This female also gave more wing flicks and flights than any robin trained using ROBMOB. The second TRAINED female gave body movements at a similar level to the two UNTRAINED and to the average of the 20 NOTRAIN robins.

Neither of the robins trained as fledglings alarm called or gave body displays towards the stoat near their nests and most time or distance comparisons were similar to those given by untrained robins (Table 4.1).

The two UNTRAINED robins did spend less time in view of the stoat than did the TRAINED robins but none of these times were outside the range of times recorded for NOTRAIN or ROBMOB trained robins.

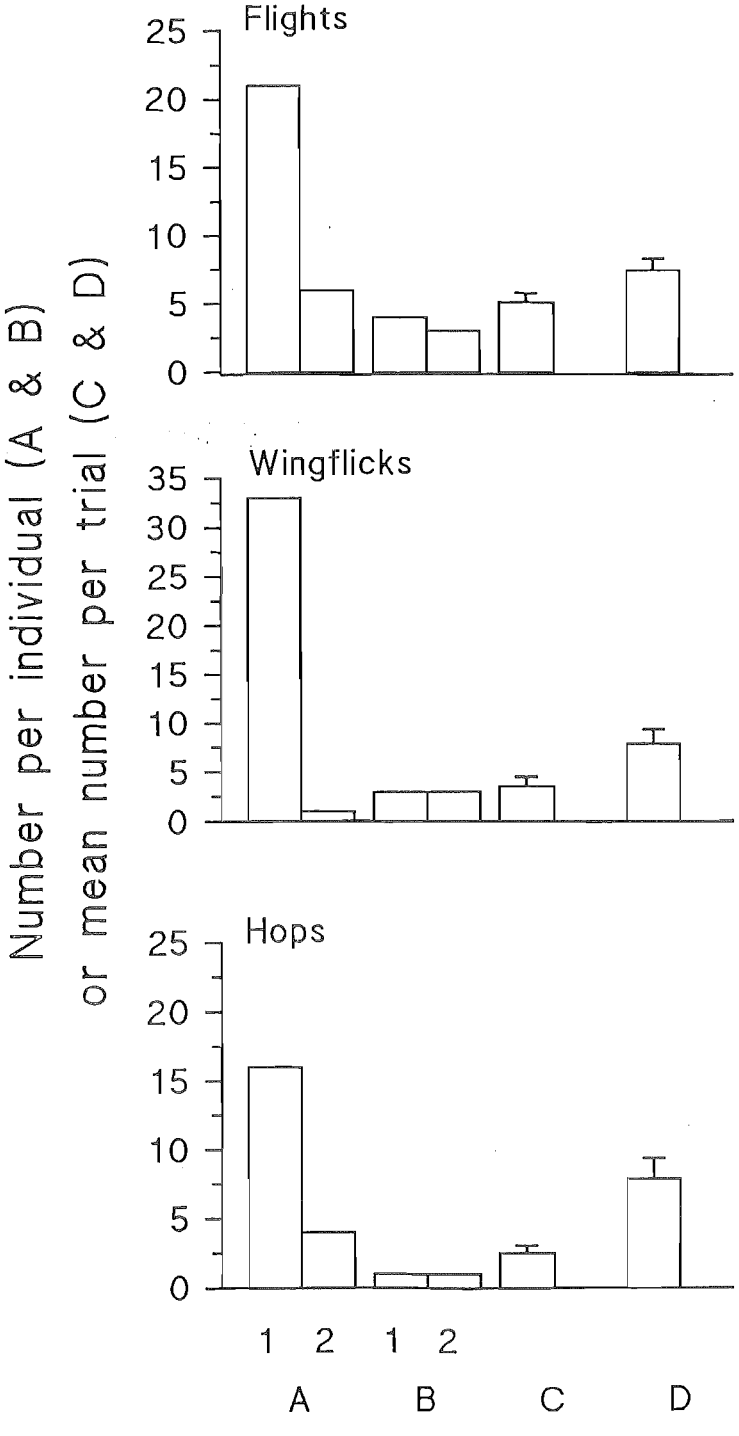


Figure 4.2: Body movement responses of fledgling and adult robins to the stoat presented at their nests. Bars A and B are individual robins, whereas C and D are mean (±se) responses by robins from the NOTRAIN and ROBMOB training regimes (N=20 per regime). Robins in A were trained as fledglings one year previously, whereas robins in B were also one year old, but were untrained as fledglings.

Table 4.1: Responses of robins TRAINED or UNTRAINED as fledglings and tested one year later as breeding adults, compared to mean (± se) responses of adult robins trained (ROBMOB, n=20) or untrained (NOTRAIN, n=20). NOTRAIN and ROBMOB descriptions and data from Chapter 3.

Variable	TRAINED 1	TRAINED 2	UNTRAINED 1	UNTRAINED 2	NOTRAIN x ± se	ROBMOB x ± se
Closest approach distance (cm)	50	150	100	50	94 ± 13.7	81 ± 13.4
Time in view of stoat+	174	220	32	16	84 ± 23.81	47 ± 44.2
Total time off nest+	568	316	150	387	310 ± 25.3	389 ± 52.1
Time on nest post-test+	240	307	115	375	458 ± 64.1	533 ± 64.7
Time off nest post-test+	56	156	20	242	196 ± 31.1	201 ± 28.0
Alarm calls	0	0	0		0	0	0
Body displays	0	0	0		0	3	12

+ measurements to ± 1 sec.

DISCUSSION

Because of the very low survival rate of fledgling robins on Motuara Island, little quantitative evidence of transferral of enemy recognition ability between generations by cultural means was obtained. The nest-defence responses of the two surviving robins who had been trained as fledglings were not similar and no definitive conclusions about the ability of fledgling robins to use learned enemy recognition and response behaviours are possible.

However, these results are encouraging. One of the two females trained as a fledgling gave one of the highest rates of body movements of any bird recorded on Motuara Island when tested as an adult. Further training and testing of fledglings should aim to identify critical learning periods (cf. song-learning, see Marler & Tamura 1964) where fledglings may be particularly receptive to learning appropriate responses to give towards enemies. By using different types and intensities of artificial training methods and training different ages of fledglings to respond to an enemy, an effective training method may be determined.

CHAPTER 5

Variation in nest-defence response due to context factors

In previous chapters I presented comparisons of nest-defence responses of robins between nests. I assumed that the intensity of the nest-defence responses of robins was related to previous training or previous natural experience with predators and not to differences caused by the context of each stimulus presentation (ie. context-specific variation, see Montgomerie & Weatherhead 1988).

A number of context-specific variables are known to affect nest-defence responses. Differences may be due to variation in bird, nest or predator-related characteristics. These include, first, differences among birds such as sex, breeding condition and age of the parent (Curio 1980, Knight *et al.* 1987, Smith *et al.* 1984, Wiklund 1990), renesting potential (Barash 1975, Biermann & Robertson 1983, Curio *et al.* 1984, Regelmann & Curio 1983, Shedd 1982), and brood size (Gottfried 1979, Greig-Smith 1980, Wallin 1987, Windt & Curio 1986); second, there may be nest-site variations such as conspicuousness, height and position of the nest in the tree (Hobson *et al.* 1988, McLean *et al.* 1986, Rickleffs 1977); and third, motivation or satiation levels of the predator may vary independently from the nest-defence response of the bird (Buitron 1983, Eden 1987). These factors and underlying theoretical models have recently been reviewed by Montgomerie & Weatherhead (1988), Redondo (1989) and McLean & Rhodes (1991).

I controlled for variation in context-variables in Chapters 2, 3 & 4 by randomising allocation of predator and control stimuli to each nest, and by using inanimate stimuli which standardized the potential threat and movement variation. For completeness, at all nests where I presented the stoat and the box, I also measured several context-variables which have been shown to affect the intensity of nest-defence responses in other studies (refs as above).

Therefore, the aim of this chapter is to determine whether robin nest-defence responses are affected by variation in some of the context-related factors which have been identified in other studies as being important determinants of the

intensity of nest-defence responses. Specifically, I correlate seven context-variables with the intensity score given towards the stoat and the box placed near robin nests.

I did not consider four context-variables that may be important determinants of robin nest-defence intensity. These were renest potential, sex and breeding condition of the responding bird, and predator behaviour. No significant relationship was found between sex and the intensity of the response of robins (analysed in Chapter 2 & 3), and as a mount of a predator was used there was also no predator-related variability between tests. I was unable to quantify either breeding condition (eg. Wiklund 1990) or renest potential (Barash 1975). The potential to renest did vary between the two populations. Robins on Motuara Island generally nested 1-2 times, whereas Kowhai Bush robins successfully raised up to 4 clutches per year (Flack 1976, unpubl. data). However, as each individual differs in its ability to renest, comparisons of nest-defence responses with renest potential should ideally be at the individual level (Redondo 1989). This requires a more detailed knowledge of life-history parameters than is currently available for these populations of robins.

METHODS

Comparisons

The intensity scores for nest-defence responses of robins towards the stoat and the box, analysed in Chapters 2 and 3 were compared to each context-variable. Details of the locality, nest-contents and stimulus used are shown in Table 5.1, and descriptions of presentation methods are given in Chapters 2 and 3.

Measurements were made of six nest-site variables and one robin-related context-variable. These were:

Nest-related variables

(i) Nest conspicuousness; measured by subjectively assessing vegetation cover at a distance of 1m from the nest. Cover was scored from four directions (using the main compass points) and from three planes (above, horizontally, below). Thus cover at each nest was scored on a 12 point scale. Nest cover was

either 0 (nest visible at 1m) or 1 (nest not visible at 1m), from each direction, so the most conspicuous nests scored 0 and the most concealed nests scored 12.

(ii) Nest height above ground level.

(iii) Nest height relative to nest-tree height.

(iv) Eight locations of nests in the nest-tree; being in primary, secondary or tertiary forks, outer leaves of canopy, crown or side of tree fern, or in cavity in tree trunk.

(v) Nest-tree species, for the five most common tree species. The remaining nests placed in a sixth general group.

(vi) Habitat type, using broad vegetation zones defined by Walls (1983) for Motuara Island and Hunt & Gill (1979), for Kowhai Bush (see Chapter 1).

Robin-related variable

(i) Brood size (number of eggs or chicks at the time of stimulus presentation).

Analyses

The intensity scores recorded from robins at each nest were regressed against brood size, nest height, relative height and conspicuousness. Comparison of intensity scores against habitat, tree species and nest location were made using Spearmans Rank Correlations.

RESULTS

Of 63 statistical comparisons, significant differences were found for only two of the nest- or robin-related variables, for one stimulus presentation type (Table 5.2). These differences were in the intensity of response towards the box at Kowhai Bush due to the height of the nest, with nest-defence increasing as nest height decreased (44% of variance explained by the correlation) and relative nest height decreased (51% of variance explained).

Table 5.1: Stimulus type, locality and nest-contents at the time of stimulus presentation, and the previous training of robins. Localities are Motuara Island (M) and Kowhai Bush (K).

Stimulus Type	Locality	Nest Contents	Previous Training*	Sample Size
Stoat	M	chicks	None	30
Box	M	chicks	None	30
Stoat	K	chicks	None	14
Box	K	chicks	None	14
Stoat	M	eggs	ROBMOB	20
Stoat	M	eggs	BKBMOB	20
Stoat	M	eggs	ALARM	20
Stoat	M	eggs	DISTRES	20
Stoat	M	eggs	NOTRAIN	20

* as described in Chapter 3.

Table 5.2: Regression (R^2), Student's t-values (t), correlation (r) and p-values for each of eight nest- and robin-related variables with intensity scores, for each stimulus presentation type. Study area and stimulus types are Motuara Island stoat (MS) and box (MB) and Kowhai Bush stoat (KS) and box (KB). Sample size as for Table 5.1.

Nest and robin related variables		Study area and stimulus MS	MB	KS	KB
Height of nest	R2	0.01	0.01	0.04	0.44
	t	- 0.3	0.4	- 0.7	- 2.8
	p	NS	NS	NS	0.02
Relative nest height	R^2	0.08	0.01	0.01	0.51
	t	- 1.6	-0.2	- 0.2	- 3.2
	p	NS	NS	NS	< 0.01
Cover score	R^2	0.11	0.01	< 0.01	0.01
	t	-1.9	-0.6	- 0.1	- 0.2
	p	NS	NS	NS	NS
Brood size	R^2	0.01	0.05	0.09	< 0.01
	t	- 0.5	1.1	- 0.6	- 0.1
	p	NS	NS	NS	NS
	n	26	26	6	6
Habitat type	r	-0.28	0.13	- 0.26	0.26
Nest location	r	-0.18	-0.01	0.36	0.09
Tree species	r	0.02	-0.16	- 0.11	- 0.11

		ROBMOB	ALARM	DISTRES	BKBMOB	NOTRAIN
Height of nest	R^2	0.03	0.01	0.02	0.01	0.01
	t	-0.2	0.2	0.6	0.3	0.4
	p	NS	NS	NS	NS	NS
Relative nest height	R^2	0.01	<0.01	<0.01	0.02	0.01
	t	0.4	-0.1	- 0.1	- 0.6	-0.3
	p	NS	NS	NS	NS	NS
Cover score	R^2	0.06	0.18	0.17	<0.01	0.10
	t	1.0	-1.9	- 1.7	- 0.2	1.5
	p	NS	NS	NS	NS	NS
Brood size	R^2	0.24	<0.01	0.01	0.17	0.01
	t	-1.7	0.2	- 0.3	- 1.5	0.2
	p	NS	NS	NS	NS	NS
	n	11	18	11	14	11
Habitat type	r	0.20	0.21	0.33	0.22	0.37
Nest location	r	0.28	-0.26	- 0.01	0.01	0.18
Tree species	r	0.03	-0.08	- 0.34	- 0.17	-0.24

DISCUSSION

These results support my initial assumption that random allocation of stimuli to each nest sufficiently controls for variation in nest-defence intensity due to context-related differences. With two exceptions, none of the nest-defence intensity scores of robins were strongly dependent on the context-variables I measured.

I offer no functional explanation as to why intensity of response to the box should decrease as absolute and relative height of the nest in the nest-tree increased. Functional relationships between response to an enemy and height of the nest have been found in other studies (see Montgomerie & Weatherhead 1988), with increased nest height being related to a decreased chance of predation and therefore a reduced need to defend the nest. However, Moors (1983) found no such relationship between height and predation levels at Kowhai Bush, and therefore nest-defence response intensity of this population should not be dependent on the height of the nest. I suggest that the relationship between response to the box and nest-height is due in part to chance factors when undertaking large numbers of statistical analyses (see Martin & Bateson 1986).

Robin nest-defence intensity scores may be correlated with many other context-variables which, in this study, I was unable to measure. However, these results indicate that random allocation of different treatments (ie. stimuli) to nests, will ensure homogeneity of variance between treatments.

CHAPTER 6

GENERAL DISCUSSION

In this study I have shown first, that robins with different levels of experience of stoats have different abilities in recognising and responding to stoat as enemies, and second, that robins who are stoat-naive are able to quickly learn to recognise the stoat as a potential enemy. I was unable to show that enemy recognition ability may be transferred between generations by cultural means, and this question remains untested.

I suggest that robins on Motuara Island, who have probably never historically seen stoats, are behaviourally representative of all robin populations (and all endemic passerines?) prior to mammalian introductions. I expand this point to suggest it is *because* of this behavioural naivety that many endemic New Zealand birds are unable to survive the introduction of the new and unrecognised mammalian predator group. This is not a new idea; many biologists have suggested that one reason for bird extinctions in New Zealand was the avifauna's inability to cope with mammalian predators (Holdaway 1989, Moors 1985, Williams 1962). However, this is the first study which has quantified recognition and response ability (or inability) towards a mammalian predator for any New Zealand bird, *before* responses have been modified through interactions with predators.

The contribution of behavioural processes to the causes of the decline of the endemic avifauna have not featured prominently in paleoecological or paleoavifaunal discussions. Most studies have focused on aspects of the ecology and breeding biology of the past avifauna (eg. see Rudge 1989) and therefore interpretations of why some populations of birds have declined are heavily biased towards morphological (eg. poor flight), breeding (eg. ground-nesting) or habitat-related deficiencies. The paucity of solid behavioural data has enhanced this bias and although explanations of the decline of endemic birds based on ecological evidence are almost certainly accurate, it may be that behavioural inadequacies in recognition and response towards mammalian predators played a far greater role in the decline of native birds than is indicated by the current evidence.

Of course, for many species now extinct or living entirely in coexistence with mammals, it is too late to measure pre-mammal behavioural responses towards mammalian predators. However, there are several island-based populations of birds that have had no historical contact with this predatory group (eg. Snares Island fernbird, *Bowdleria punctata caudata*, black tit, *Petroica macrocephala dannefaerdi*, Chatham Island tit, *P.m. chathamensis*, Chatham Island black robin, *P. traversi*). These populations can provide invaluable information on behavioural recognition and response abilities, not only in giving a better understanding of New Zealand's past avifauna, but also as a means of developing future endangered species management strategies and as a test case for theoretical cognitive models used to examine issues of enemy recognition and response.

Robins without experience of mammalian predators have weak recognition and response abilities, indicating that they may lack the genetic bases for recognition (perceptual and stored representations of the cognitive model of enemy recognition described by McLean & Rhodes 1991, Fig 1.1b), or indicating that they may "recognise" the enemy, but fail to make an association between the enemy and potential threat. The low response towards the stoat was not due to naive robins having a reduced behavioural repertoire, which lacked strong nest-defence behaviours. Robins on Motuara Island were observed to alarm call, and they gave all of the displays recorded from mainland populations when I approached nests to band chicks.

Because measures of recognition are usually made indirectly by measuring response (but see Mueller & Parker 1980) it may be difficult to separate "failure to recognise" from "recognition but failure to respond". However, robins learned responses to the stoat after one brief previous experience with that predator and it is more likely that naive robins lack only the association between a stoat and the threat that a stoat represents.

The decline of naive birds during initial interactions with unfamiliar predators may be attributed to two factors. First, in terms of the Predatory Imminence Continuum model (Fanselow & Lester 1988), naive birds may be susceptible to predation because of their behaviours in the stage before encountering a predator, the "pre-encounter defensive" stage (Fig 1.1a). Experienced birds at this stage of

the continuum would normally modify activity patterns (eg. feeding in the day-time to avoid nocturnal predators) and spend more time engaged in behaviours, such as vigilance, to reduce the probability of interacting with a mammalian predator. The level and type of pre-encounter defensive behaviour will "...reflect the likelihood of encountering a predator." (Fanselow & Lester 1988, p.188). As New Zealand birds evolved in an environment free from mammalian predators, there was no need to develop (or retain) pre-encounter defensive behaviours. Therefore, when the mammalian predators arrived in New Zealand, the birds were vulnerable to predation because they did not expect predators to be present (ie. they lacked awareness of mammalian predators). Second, New Zealand birds may have also been unaware of appropriate responses, once a mammalian predator was encountered. Well-developed nest-defense strategies of the birds in this "post-encounter defensive" stage (Fig 1.1a) may increase the chance of survival of the bird or its offspring, but I have shown that at least one endemic New Zealand bird, the robin, responds towards a novel mammalian predator with weak nest-defence behaviours. I suggest that weak defensive responses were a common trait among all endemic New Zealand birds prior to contact with any of the introduced mammalian predators.

Mainland robins coexist successfully with stoats, and they respond to stoats with behaviours that are significantly stronger than robins that have not been exposed to this predator. Nest-defence responses are therefore likely to be an important anti-predator defence mechanism in this species, as has been found in other species (Andersson *et al.* 1980, Greig-Smith 1980, Murphy 1983, Pettifor 1990, Temrin & Jakobsson 1988, other examples in Chapter 1). By increasing the probability of survival, strong nest-defence responses may therefore be critical to the facilitation of continued stoat-robin coexistence.

Robins being able to coexist with mammalian predators augurs well for their long-term future survival. Other endemic New Zealand species do not coexist with some or all of the introduced suite of mammalian predators (eg. stitchbird, *Notiomystis cincta*, saddleback, *Philesturnus carunculatus*, kakapo, *Strigops habroptilus*). Such species are restricted to mammalian predator-free islands and because of this restriction their long-term survival must always be at risk (see Moors

1985).

I have shown that it is possible to increase artificially the behavioural responses of one endemic species towards a mammalian predator. I suggest that such training can be more generally applied (ie. if more species have the ability to learn nest-defence responses when provided with the experience), and that this technique will allow the reintroduction of island-restricted birds to areas with predators. Therefore artificial training techniques should be considered as an option in the future management of endangered species.

Careful consideration must be given to the design of training regimes, with researchers developing regimes that are specific to the situation each bird species faces. The predator used in training must be a major predator of the trainee bird species *and* it must be frequently encountered in the birds temporal and spatial environment. For example, training a bird to give nest-defence responses to nocturnal predators (eg. rats) may not be as effective as training birds to respond to more diurnal or crepuscular predators (eg. cats and stoats). Similarly, training may not be effective if a predator that hunts entirely on the ground (eg. ferrets) is used in a training regime targeted at an arboreal-living bird. An effective training design should incorporate as many details of the target birds' defence-responses as possible, including both audible and visual cues provided by conspecific mounts and calls. Perhaps most importantly, the presence of conspecific birds in the training regime should depend on the response of the target species to intruders in its territory.

I believe that training techniques have greatest application in situations where captive-reared species, raised in isolation and safety from mammalian predators are given realistic simulated experiences with predators before being released. Once in the wild the experiences gained in training may enhance survival of the newly released birds through the critical post-release period. Furthermore, these enhanced nest-defence responses may be transferred to offspring culturally, and in this way enemy recognition and response behaviours can be maintained in the population.

ACKNOWLEDGEMENTS

I thank the Ornithological Society of New Zealand, University of Canterbury grant to Dr. Ian McLean, and Grandma for funding to support travel and equipment costs. Drs. John Warham and Ian McLean jointly convinced me that work on the nocturnal sooty shearwater was a good way to fill in my spare time (ie. those long nights when robins sleep) and thereby fund the robin research in 1990. The Toyota Foundation of Japan kindly provided the money to do so.

I thank the Department of Conservation (DoC) for permission to work and live on Allports and Motuara Island, and for logistic support, use of equipment and providing some (of the many) colour-bands now attached to robins. The DoC Banding Office gave permission to band robins. Thanks to the staff of the Picton and Nelson DoC, in particular, to Derek Brown, Bill Cash, Roy Grose and Kath Walker for making the island trips that much easier.

Thanks to Jack van Berkyl for permission to stay at the Edward Percival Field Station in Kaikoura and to Fiona Proffitt for getting lost with me in the "real" Kowhai Bush, where the robins hang-out.

Many (many) people provided help, company, bread, pizza's and red wine in the field. These were: Wayne Linklater, Ian McLean and Nikki Wells on Allports Island, Rebecca Brown, Simon Bulman, Heather Cameron, Lindsay Chadderton, Warren Chinn, Andrew Le Beau, Ian McLean, Rachel Mulligan, Fiona Proffitt, Stephanie Tulloch, John Warham, Sue Waugh and Nikki Wells on Motuara Island, and Ian McLean, and Nikki Wells at Kowhai Bush. It was great having them to stay...but I accept no responsibility for the physical damage (eg. dead knees, unintentional dunkings in the sea) that some had to endure. Special thanks to Lindsay, who made the robins on the east and south side of the island (and the kitchen) his own, allowing me to get on with scaring the birds and talking to myself.

Travel to Motuara and Allports Islands was made easy using "Beachcombers" and "Travel Stop" boats, in varying weather conditions and at varying speeds, but always with friendly and efficient service; I thank them for tolerating endless equipment and bodies, flung on board at great haste.

Many thanks to neighbours, Dave and Sandra Baker of Cape Jackson Farm, for

watching over me while on Motuara Island. It was reassuring to have two great people so close at hand if ever I needed anything. Special thanks to them both for the interest in the study, the nightly conversations, the messages, the beers, the oysters! (etc. etc.).

I thank the technical and secretarial staff for support, and in particular, to Franz Ditz, Dave Greenwood, Bruce Lingard and Dave Tattle for "preparing" me for the field. Thanks also to Bruce for meeting my endless and unorganised requests for stores, and for getting me and my gear to Picton on time.

Many people have discussed various aspects of this study with me, but in particular, the fortnightly Behavioural Ecology group meetings and the 1990 Behaviour and Ecology Workshop in Rotorua were a source of many stimulating conversations and ideas. Thanks to all the participants.

I thank Robert Jackson, Andrew Le Beau, Ian McLean, Rachel Mulligan and Kathyriney Taylor, for reading various drafts of the thesis, and for making me make it make some sort of sense. Rachel also got to play with my graphs (thank you!).

The idea that it may be feasible to train naive New Zealand birds to respond to mammalian predators was Dr. Ian McLeans. Thanks Ian for entrusting me with "your baby" and for giving me the freedom to develop it as I wished. I hope I have done it justice. Also, many thanks - for the encouragement and support over the last few years, and for making my life easier when it wasn't.

What can I say Nik? Much of this study was undertaken with the love and encouragement of Nikki Wells, *Y por mejores tiempos en el futuro!*

LITERATURE CITED

Alcock, J. 1984. *Animal behaviour: an evolutionary approach.* 3rd edition. Sinauer Associates Inc. Sunderland, Mass. 596 pp.

Alder, E.M. 1975. Genetic and maternal influences on docility in the skomer vole, *Clethrionomys glareolus skomerensis. Behavioural Biology*, **13**, 251-255.

Altmann, S.A. 1956. Avian mobbing behaviour and predator recognition. *Condor*, **58**, 241-253.

Andersson, M., & Wiklund, C.G. 1978. Clumping versus spacing out: experiments on nest predation in fieldfares, *Turdus pilaris. Anim. Behav.*, **26**, 1207-1212.

Andersson, M., Wiklund, C.G., & Rundgren, H. 1980. Parental defence of offspring: A model and an example. *Anim. Behav.*, **28**, 536-542.

Armstrong, E.A. 1954. The ecology of distraction display. *Brit. J. Anim. Behav.*, **2**, 121-135.

Atkinson, I.A.E. 1973. Spread of ship rats, *Rattus r. rattus* L., in New Zealand. *J. Royal Soc. N.Z.*, **3**, 457-472.

Atkinson, I.A.E. 1985. *The spread of commensal species of Rattus to oceanic islands and their effects on island avifaunas.* pp 35-84 in: Moors, P.J. (ed). *Conservation of island birds. Case studies for management of threatened island species.* ICBP Tech. Publ., **3**. Norwich, England.

Barash, D.P. 1975. Mobbing behaviour by crows: the effect of the "crow-in-distress" model. *Condor*, **74**, 120.

Biermann, G.C. & Robertson, R.J. 1983. Residual reproductive value and parental investment. *Anim. Behav.*, **31**, 311-312.

Blancher, P.J., & Robertson, R.J. 1982. Kingbird aggression: does it deter predation? *Anim. Behav.*, **30**, 929-930.

Bolles, R.C. 1970. Species-specific defence reactions and avoidance learning. *Psychological Review*, **77**, 32-48.

Brunton, D.H. 1986. Fatal anti-predator behaviour of a killdeer. *Wilson Bull.*, **98**, 605-607.

Buitron, D. 1983. Variability in the responses of black-billed magpies to natural predators. *Behaviour*, **78**, 209-236.

Buller, W.L. 1882. *Manual of the birds of New Zealand.* Govt. Printer. Wellington.

Byrkjedal, I. 1987. Anti-predator behaviour and breeding success in greater golden plover and Eurasian Dotterel. *Condor*, **89**, 40-47.

Caldwell, G.S. & Rubinoff, R.W. 1983. Avoidance of venomous sea snakes by naive herons and egrets. *Auk*, **100**, 486-489.

Chandler C.R. & Rose R.K. 1988. Comparative analysis of the effects of visual and auditory stimuli on avian mobbing behaviour. *J. Field Ornithol.*, **59**, 269-277.

Coleman, R.M. 1987. Does experience with predators affect parental investment? *Auk*, **104**, 791-792.

Conover, M.R. 1987. Acquisition of predator information by active and passive mobbers in ring-billed gull colonies. *Behaviour*, **102**, 41-57.

Coss, R.G. & Owings, D.H. 1978. Snake-directed behaviour by snake naive and experienced California ground squirrels in a simulated burrow. *Z. Tierpsychol.*, **48**, 421-435.

Curio, E. 1975. The functional organisation of anti-predator behaviour in the pied flycatcher: a study of avian visual perception. *Anim. Behav.*, **23**, 1-115.

Curio, E. 1978. The adaptive significance of avian mobbing. I. Teleonomic hypothesis and predictions. *Z. Tierpsychol.*, **48**, 175-183.

Curio, E. 1980. An unknown determinant of a sex-specific altruism. *Z. Tierpsychol.*, **53**, 139-152.

Curio, E., Ernst, U. & Vieth, W. 1978a. The adaptive significance of avian mobbing: II. Cultural transmission of enemy recognition in blackbirds: effectiveness and some constraints. *Z. Tierpsychol.*, **48**, 184-202.

Curio, E., Ernst, U. & Vieth, W. 1978b. Cultural transmission of enemy recognition: one function of mobbing. *Science*, **202**, 899-901.

Curio, E. & Regelmann, K. 1986. Predator harassment implies a real deadly risk: a reply to Hennessy. *Ethology*, **72**, 75-78.

Curio, E., Regelmann, K. & Zimmermann, U. 1984. The defence of first and second broods by great tits *Parus major*: a test of predictive sociobiology. *Z. Tierpsychol.*, **66**, 101-127.

Dawkins, R. & Krebs, J.R. 1978. *Animal signals: information or manipulation?* pp 282-309 in: Krebs, J.R. & Davies, N.B. (eds). *Behavioural ecology*. Blackwell, Oxford.

Dean, S.L. 1989. *Mixed species flocks of insectivorous birds in Kowhai Bush, Kaikoura.* Unpubl. MSc. thesis, University of Canterbury.

Denson, R.D. 1979. Owl predation on a mobbing crow. *Wilson Bull.*, **91**, 133.

Dörner, D. 1982. *The ecological conditions of thinking.* pp 95-112 in: Griffin, D.R. (ed). *Animal mind - human mind.* Springer-Verlag, Berlin, Heidelberg, New York.

Eden, S.F. 1987. The influence of carrion crows on the foraging behaviour of magpies. *Anim. Behav.*, **35**, 608-610.

Edmunds, M. 1974. *Defence in animals. A survey of anti-predator defences.* Longman Gp. Ltd. Essex. 357 pp.

Ellis, D.H., Dobrott, S.J. & Goodwin, J.G.Jnr. 1977. *Reintroduction techniques for masked bobwhites.* pp 345-354 in: Temple, S.A. (ed). *Endangered birds. Management techniques for preserving threatened species.* Croom Helm Ltd. London.

England, M.E. 1986. Harrier kills mobbing willet. *Raptor Research*, **20**, 78-79.

Fanselow, M.S. & Lester, L.S. 1988. *A functional behaviouristic approach to aversively motivated behaviour: predatory imminence as a determinant of the topography of defensive behaviour.* pp 185-212 in: Bolles, R.C. & Beecher, M.D. (eds). *Evolution and learning.* Lawerence Erlbaum Ass. London.

Findlay, C.S. 1991. Fundamental theorem of natural selection under gene-culture transmission. *Proc. Natl. Acad. Sci.*, **88**, 4874-4876.

Fisher, R.A. 1930. *The genetic theory of natural selection.* Claredon Press, Oxford, England.

Flack, J.A.D. 1974. *Chatham Island black robins.* pp 25-31 in: *Wildlife, a review.* no 5.

Flack. J.A.D. 1975. Aspects of the ecology of the New Zealand Robin, *Petroica australis. Emu*, **74**, 286.

Flack, J.A.D. 1976. The use of frontal spot and crown feathers in inter- and intraspecific display by the South Island robin, *Petroica australis australis. Notornis*, **23**, 90-105.

Flack, J.A.D. 1977. Interisland transfers of New Zealand black robins. pp 365-372 in: Temple, S.A. (ed). *Endangered birds. Management techniques for preserving threatened species.* Croom Helm Ltd. London.

Flack, J.A.D. 1979. *Biology and ecology of the South Island robin.* pp 22-26 in: Hunt,

D.M. & Gill, B.J. (eds). *Ecology of Kowhai Bush, Kaikoura*. Mauri Ora, 2, Spec. publ., University of Canterbury Biological Soc., Christchurch.

Flack, J.A.D. 1985. *Robin*. pp 282-283 in: *Reader's Digest Complete book of New Zealand Birds*. Reed Methuen, Sydney.

Flack, J.A.D. & Lloyd, B.D. 1978. *The effect of rodents on the breeding success of the South Island robin*. pp 59-66 in: Dingwall, P.R., Atkinson, I.A.E. & Hay, C. (eds). *The ecology and control of rodents in New Zealand nature reserves. Proceedings of a symposium convened by the Lands & Survey Dept.* Info. series No. 4. L & S. Dept. Wellington, NZ.

Fleming, C.A. 1950. New Zealand flycatchers of the genus *Petroica* Swainson: Part I & II. *Trans. Roy. Soc. N.Z.*, **78**, 14-47, 127-160.

Gottfried, B.M. 1979. Anti-predator aggression in birds nesting in old field habitats: an experimental analysis. *Condor*, **81**, 251-257.

Greig-Smith, P.W. 1980. Parental investment in nest-defence by stonechats, *Saxicola torquata*. *Anim. Behav.*, **28**, 604-619.

Guthrie-Smith, H. 1925. *Bird life on island and shore*. William Blackwood & Sons. Edinburgh & London.

Gyger, M., Karakashian, S.J. & Marler, P. 1986. Avian alarm calling: is there an audience effect? *Anim. Behav.*, **34**, 1570-1572.

Hammerstrom, F. 1957. The influence of a hawk's appetite on mobbing. *Condor*, **59**, 192-194.

Hauser, M.D. 1988. How infant vervet monkeys learn to recognize starling alarm calls: the role of experience. *Behaviour*, **103**, 187-201.

Hay, R. 1975. *The vocal behaviour of the New Zealand robin, Petroica australis, and its local congenerics*. Unpubl. MSc. thesis, University of Auckland.

Heaphy, C. 1842. *Narrative of a resident in various parts of New Zealand*. Swath, Elder & Co. 65, Cornhill.

Hennessy, D.F. 1986. On the deadly risk of predator harassment. *Ethology*, **72**, 72-74.

Hirsch, S.M. & Bolles, R.C. 1980. On the ability of prey to recognize predators. *Z. Tierpsychol.*, **54**, 71-84.

Hobson, K.A., Bouchart, M.L. & Sealy, G.S. 1988. Responses of naive yellow warblers to a novel nest predator. *Anim. Behav.*, **36**, 1823-1830.

Holdaway, R.N. 1989. New Zealand's pre-human avifauna and its vulnerability. pp 11-26 in: Rudge, M.R. (ed). Moas, mammals and climate in the ecological history of New Zealand. *N.Z. J. Ecol.*, **12** (suppl).

Hunt, D.M. & Gill, B.J. 1979. Ecology of Kowhai Bush, Kaikoura. *Mauri Ora*, **2**, Spec. publ., University of Canterbury, Christchurch.

King, C.M. 1984. *Immigrant killers: introduced predators and the conservation of birds in New Zealand.* Oxford University Press, Auckland. 224 pp.

Klix, F. 1982. *On the evolution of cognitive processes and performances.* pp 225-250 in: Griffin, D.R. (ed). *Animal mind - human mind.* Springer-Verlag, Berlin, Heidelberg, New York.

Klopfer, P.H. 1957. An experiment on emphatic learning in ducks. *Am. Nat.*, **91**, 61-63.

Klump, G.M. & Shalter, M.D. 1984. Acoustic behaviour of birds and mammals in the predator context. *Z. Tierpsychol.*, **66**, 189-226.

Knight, R.L. 1984. Responses of nesting ravens to people in areas of different human densities. *Condor*, **86**, 345-346.

Knight, R.L. & Temple, S.A. 1986a. Why does intensity of avian nest defence increase during the nesting cycle. *Auk*, **103**, 318-327.

Knight, R.L. & Temple, S.A. 1986b. Methodological problems in studies of avian nest defence. *Anim. Behav.*, **34**, 561-566.

Knight, R.L., Grout, O.J. & Temple, S.A. 1987. Nest-defence behaviour of the American crow in urban and rural areas. *Condor*, **89**, 175-177.

Kruuk, H. 1976. The biological function of gulls' attraction towards predators. *Anim. Behav.*, **24**, 146-153.

Lüer, G. 1982. *Problem solving.* pp 159-176 in: Griffin, D.R. (ed). *Animal mind - human mind.* Springer-Verlag, Berlin, Heidelberg, New York.

Lumsden, C. & Wilson, E.O. 1981. *Genes, mind and culture.* Harvard University Press, Cambridge, Mass.

M'Lean, J.C. 1911. Bush-birds of New Zealand. *Emu*, **11**, 65-78.

Markl, H. 1985. *Manipulation, modulation, information, cognition: some of the riddles of communication.* pp 163-194 in: Hölldobler, B. & Lindaeur, M. (eds). *Experimental behavioural ecology and sociobiology.* Sinauer Ass. Inc. Sunderland, USA.

Marler, P. & Peters, S. 1977. Selective vocal learning in a sparrow. *Science*, **198**, 519-521.

Marler, P. & Tamura, M. 1964. Culturally transmitted patterns of vocal behaviour in sparrows. *Science*, **146**, 1483-1486.

Martin, P. & Bateson, P. 1986. *Measuring behaviour: an introductory guide.* Cambridge University Press, Sydney. 200 pp.

McDowall, R.M. 1969. Extinction and endemism in New Zealand birds. *Tuatara*, **17**, 1-12.

McLean, I.G. 1987. Response to a dangerous enemy: should a brood parasite be mobbed? *Ethology*, **75**, 235-245.

McLean, I.G. & Maloney, R.F. 1989. Genetic and cultural factors in enemy recognition by an island-endemic bird. *Pres. to 21st International Ethological Congress*, Utrecht, Netherlands.

McLean, I.G. & Rhodes, G. 1991. *Enemy recognition and response in birds.* pp 173-211 in: Power, D.M. (ed). *Current Ornithology*, **8**. Plenum Press, New York.

McLean, I.G., Smith, J.N.M., Stewart, K.G. 1986. Nest exposure and breeding success in the American robin. *Behaviour*, **96**, 171-186.

Montgomerie, R.D. & Weatherhead, P.J. 1988. Risks and rewards of nest-defence by parent birds. *Quart. Rev. Biol.*, **63**, 167-187.

Moors, P.J. 1979. Mammal populations in Kowhai Bush., pp 35-40 in: Hunt, D.M. & Gill, B.J. (eds). *Ecology of Kowhai Bush, Kaikoura*. Mauri Ora, **2**, Spec. publ., University of Canterbury Biological Soc., Christchurch.

Moors, P.J. 1983. Predation by mustelids and rodents on the eggs and chicks of native and introduced birds in Kowhai Bush, New Zealand. *Ibis*, **125**, 137-154.

Moors, P.J. (ed) 1985. *Conservation of island birds. Case studies for the management of threatened island species.* ICBP Tech. Publ., **3**. England.

Morrell, W.P. (ed) 1958. *Sir Joseph Banks in New Zealand (from his journal).* A.H. & A.W. Reed. Wellington.

Morse, D.H. 1980. Chapter 5 in: *Behavioural mechanisms in ecology.* Harvard University Press.

Mueller, H.C. & Parker, P.G. 1980. Naive ducklings show different cardiac response to hawk than to goose models. *Behaviour*, **74**, 101-113.

Murphy, M.T. 1983. Nest success and nesting habits of eastern kingbirds and other flycatchers. *Condor*, **85**, 208-219.

Myers, J.P. 1978. One deleterious effect of mobbing in the southern lapwing, *Vanellus chilensis*. *Auk*, **95**, 419-420.

Nice, M.M. & Pelkwyk, J.T. 1941. Enemy recognition by the song sparrow. *Auk*, **58**, 195-214.

Nichols, J.D., Percival, H.F., Coon, R.A., Conroy, M.J., Hensler, G.L. & Hines, J.E. 1984. Observer visitation frequency and success of mourning dove nests: a field experiment. *Auk*, **101**, 356-358.

Oliver, W.R.B. 1930. *New Zealand Birds*. A.W. & A.H. Reed. Wellington.

Owings, D.H. & Coss, R.G. 1977. Snake mobbing by California ground squirrels: adaptive variation and ontogeny. *Behaviour*, **62**, 50-69.

Pettifor, R.A. 1990. The effects of avian mobbing on a potential predator, the European kestrel, *Falco tinnunculus*. *Anim. Behav.*, **39**, 821-827.

Pettingill, O.S. Jnr. 1976. Observed acts of predation on birds in Northern Lower Michigan. *The Living Bird*, **15**, 33-41.

Poiani, A. & Yorke, M. 1989. Predator harassment: more evidence on the deadly risk. *Ethology*, **83**, 167-169.

Pomeroy, D. 1990. Why fly? The possible benefits for lower mortality. *Biol. J. Linn. Soc.*, **40**, 53-65.

Powlesland, R.G. 1980. *Time-budget study of South Island robins, Petroica australis australis, at Kowhai Bush, Kaikoura*. Unpubl. PhD. thesis, University of Canterbury.

Pugesek, B.H. 1983. The relationship between parental age and reproductive effort in the Californian gull, *Larus californicus*. *Behav. Ecol. Sociobiol.*, **13**, 161-171.

Redondo, T. 1989. Avian nest-defence: theoretical models and evidence. *Behaviour*, **111**, 161-195.

Reed, A.H. & Reed, A.W. (eds) 1969. *Captain Cook in New Zealand*. A.H. & A.W. Reed. Wellington, Sydney.

Regelmann, K. & Curio, E. 1983. Determinants of brood defence in the great tit, *Parus major* L. *Behav. Ecol. Sociobiol.*, **13**, 131-145.

Regelmann, K. & Curio, E. 1986. Why do great tit, *Parus major*, males defend their broods more than females do? *Anim. Behav.*, **34**, 1206-1214.

Reischek, A. 1930. *Yesterdays in Maoriland. New Zealand in the 'eighties.* (Translated & edited by H.E.L. Priday). Jonathan Cape, Thirty Bedford Square, London.

Ricklefs, R.E. 1977. Reactions of some Panamanian birds to human intrusion at the nest. *Condor*, **79**, 376-379.

Riechert, S.E. & Hedrick, A.V. 1990. Levels of predation and genetically based anti-predator behaviour in the spider, *Agelenopsis aperta. Anim. Behav.*, **40**, 679-687.

Robinson, S.R. 1980. Anti-predator behaviour and predator recognition in Belding's ground squirrels. *Anim. Behav.*, **28**, 840-852.

Rudge, M.R. (ed) 1989. Moas, mammals and climate in the ecological history of New Zealand. *N.Z. J. Ecol.*, **12** (suppl), 169 pp.

Seyfarth, R. & Cheney, D. 1990. The assessment by vervet monkeys of their own and another species' alarm calls. *Anim. Behav.*, **40**, 754-764.

Shedd, D.H. 1982. Seasonal variation and function of mobbing and related anti-predator behaviour of the American robin, *Turdus migratorius. Auk*, **99**, 342-346.

Shields, W.M. 1984. Barn swallow mobbing: self defence, collateral kin defence, group defence or parental care. *Anim. Behav.*, **32**, 132-148.

Smith, W.J. 1977. *The behaviour of communicating: an ethological approach.* Harvard University Press, Cambridge, Mass. USA.

Smith, N.M., Arcese, P. & McLean, I.G. 1984. Age, experience and enemy recognition by wild song sparrows. *Behav. Ecol. Sociobiol.*, **14**, 101-106.

Soper, M.F. 1972. *New Zealand Birds.* Whitcombe & Tombs, Christchurch. 251 pp.

Taylor, K.J. 1991. *Nest defence as parental care in the grey warbler and rifleman.* Unpubl. MSc. thesis, University of Canterbury.

Temple, S.A. 1977a. *Reintroducing birds of prey to the wild.* pp 355-364 in: Temple, S.A. (ed). *Endangered birds. Management techniques for preserving threatened species.* Croom Helm Ltd., London.

Temple, S.A. 1977b. *Manipulating behavioural patterns of endangered birds: a potential management technique.* pp 435-446 in: Temple, S.A. (ed). *Endangered birds. Management techniques for preserving threatened species.* Croom Helm Ltd.,

London.

Temrin, H. & Jakobsson, S. 1988. Female reproductive success and nest predation in polyterritorial wood-warblers, *Phylloscopus siblatrix. Behav. Ecol. Sociobiol.*, **23**, 225-231.

Thornhill, R. 1989. Nest-defence by red jungle fowl, *Gallus gallus spadiceus*, hens: the roles of renesting potential, parental experience and brood reproductive value. *Ethology*, **83**, 31-42.

Toates, F.M. 1983. *Models of motivation.* pp 168-196 in: Halliday, T.R. & Slater, P.J.B. (eds). *Animal behaviour. 1. Causes and effects.* Blackwell Scientific Publ., London.

Trivers, R.L. 1972. Parental investment and sexual selection. pp 136-179 in: *Sexual selection and the descent of man. 1871-1971.* Campbell, B. (ed). Heinemann, London.

Vieth, W., Curio, E., & Ernst, U. 1980. The adaptive significance of avian mobbing. III. Cultural transmission of enemy recognition in blackbirds: cross-species tutoring and properties of learning. *Anim. Behav.*, **28**, 1217-1229.

Walker, D.G. 1983. Golden eagle killing mobbing carrion crows. *Brit. Birds*, **76**, 312.

Wallin, K. 1987. Defence as parental care in tawny owls, *Strix aluco. Behaviour*, **102**, 213-230.

Walls, G.Y. 1983. *Motuara Island scenic and historical reserve.* Internal report for the Dept. of Lands & Survey.

Weatherhead, P.J. 1979. Do savannah sparrows commit the concorde fallacy? *Behav. Ecol. Sociobiol.*, **5**, 373-381.

Wiklund, C.G. 1990. The adaptive significance of nest defence by merlin, *Falco columbarius*, males. *Anim. Behav.*, **40**, 244-253.

Williams, G.R. 1962. Extinction and the land and freshwater-inhabiting birds of New Zealand. *Notornis*, **10**, 15-32.

Wilson, D.C. 1877. Disappearance of the small birds of New Zealand. *Trans. N.Z. Instit.*, **10**, 239-242.

Windt, W. & Curio, E. 1986. Clutch defence in great tit, *Parus major*, pairs and the concorde fallacy. *Ethology*, **72**, 115-142.

Appendix 1: Techniques used in this study to find robin nests.

Robin nests were found using four methods. These were:

(1) by searching in likely nesting places, eg. tree forks, tree fern crowns;
(2) by listening for the begging calls of chicks in the nest.
(3) by following males until they carried food to the nest or to the female, or by following females to the nest;
(4) by feeding the male dead mealy worm larvae, *Tenebrio* sp., which he would take either to an incubating female, or to the nest to feed chicks. On finding *Tenebrio*, males would generally consume up to seven 1g larvae before collecting and holding extra larvae in their bill. Birds that held larvae towards the bill tip nearly always stored the food nearby for future use (see Powlesland 1980); whereas males that had incubating mates or nests with chicks held larvae towards the bill base. On collecting 1-7 larvae the male would fly in the approximate direction of the nest, giving a standard feeding phrase (Hay 1975, p75) at regular intervals. If the female was incubating she would either fly directly to the male when he was within 3-15m, or she would fly to a nearby perch and emit a series of juvenile-like begging calls (Hay 1975, p26). The male then feeds her and she goes either directly back to the nest or forages nearby for 1-15 mins before returning to the nest with a combination of short flights and pauses. I usually found nests by observing the direction and height at which the female approached the male or by sitting quietly, 5-20m from where I thought the nest was and watching a females return.

If the male was feeding chicks, his nest-approach flight was rapid and direct, sometimes from up to 30m away. Adults feeding chicks tended to move hurriedly about but once attracted to a *Tenebrio* food source they would make repeated trips between the food source and nest. If no birds were present in an area I wished to search I would either sit quietly for up to half an hour until a robin showed up, or I would try to attract birds to me by banging sticks on the ground, throwing litter about and shaking trees. A combination of these methods seemed to be most effective.

All nests were marked by a numbered plastic tag tied to a nearby tree.

Appendix 2: Techniques used in this study to catch and band robins.

Robins in all study areas were banded with a serially numbered stainless steel or aluminium C-sized butt-ended band and a unique combination of up to three C-sized colour-bands (maximum of two bands per leg). To allow quick recognition of age classes adults were banded with metal on the right leg, and sub-adults with metal on the left leg. Chicks less than 10 days old were metal-banded and were caught and colour bands added after fledging.

Robins were caught in three ways:

1) By hand. 5 -20 day old chicks were trapped in the nest.
2) By "clap-trap". On Allports Island I caught most birds using this method. I found the trap moderately slow to set-up and use, and apparently stressful for the ensnared bird. I therefore designed and used a small hand-net for all subsequent captures.
3) By hand-net, described as follows: Net-frame, #10 fencing wire (300mm diameter). Net, black plastic mesh (30mm grid) shaped and tied to be slightly concave. Handle, (1.2m long, 20mm diameter). Robins were caught by throwing a few Tenebrio larvae onto an area of disturbed litter, while holding the net about 0.5m above the spot. When the robin landed on-site the net was quickly dropped onto it. Typically, the interval between an individuals capture and its removal from the net was 30-60 secs. Because a hand-net is portable, easy to set-up and causes minimal stress to the birds I recommend its future use for capture of robins.

Once caught, birds were banded, measured and released. Measurements taken were:

1) weight, to ± 0.5g using Avinet 100g scales;
2) bill length (tip to base of first feather), width and depth (at the top of the nares);
3) tarsus length, to ± 0.1mm using Mitutoyo calipers (from notch to grove) and;
4) wing length to ±1mm (flattened not straightened).

Appendix 3: Colour-band combinations, sex and age of robins presented with the stoat and the box (STBX), trained (regimes ROBMOB, ALARM, DISTRES, BKBMOB, NOTRAIN), or robins present during fledgling training (FT). (*) indicates tests completed in 1989, all other tests completed in 1990.

Motuara Island

Bands	Sex	Age	Test		Bands	Sex	Age	Test	
R/M	F	A	ROBMOB*		WY/WM	F	A	ROBMOB	
LG/M	M	A	ALARM		WR/WM	F	A	STBX	
WY/M	F	A	BKBMOB		YLG/WM	M	A	DISTRES	
WR/M	M	A	BKBMOB		YDG/WM	M	A	STBX	FT*
WDG/M	F	A	STBX	FT*	RW/WM	F	A	BKBMOB*	
WB/M	M	A	STBX*		RLG/WM	F	A	ROBMOB	
YW/M	M	A	ALARM*		RDG/WM	M	A	ROBMOB	
YR/M	M	A	ROBMOB*		LGR/WM	F	A	ALARM	
YLG/M	F	A	ROBMOB*		DGW/WM	M	A	DISTRES	
YDG/M	M	A	STBX		DGR/WM	M?	A	STBX	FT*
YB/M	F	A	STBX		BW/WM	M	A	ROBMOB	
RLG/M	M	A	ROBMOB*		BY/WM	M	A	NOTRAIN	
RB/M	M	A	STBX*		BR/WM	M	A	ALARM	
LGY/M	M	A	DISTRES		BLG/WM	M	A	ALARM	
LGDG/M	M	A	STBX	FT*	WB/YM	F	A	NOTRAIN	
DGY/M	M	A	ROBMOB		YW/YM	M	A	BKBMOB	
DGLG/M	M	A	STBX	FT*	YLG/YM	M	A	ROBMOB*	
DGB/M	F	A	STBX	FT*	YB/YM	M	A	STBX	
BW/M	M	A	STBX		RY/YM	M	A	BKBMOB	FT*
Y/WM	F	A	STBX	FT*	RB/YM	F	A	DISTRES	
B/WM	F	A	ALARM*		LGY/YM	M	A	BKBMOB	FT*
W/YM	F	A	DISTRES		LGR/YM	M	A	NOTRAIN	
B/YM	F	A	STBX*		LGB/YM	F	A		FT*
B/RM	M	A	NOTRAIN		DGY/YM	M	A		FT*
W/LGM	F	A	ROBMOB		DGR/YM	M	A	BKBMOB	
Y/LGM	M	A	ROBMOB		DGLG/YM	F	A	STBX	FT*
R/LGM	M	A	STBX*		DGB/YM	M	A	ALARM	FT*
LG/LGM	M	A	ROBMOB*		BW/YM	M	A	STBX	FT*
DG/DGM	F	A	BKBMOB	FT*	BY/YM	F	A	NOTRAIN	
B/DGM	M	A	BKBMOB	FT*	BR/YM	M	A	STBX	FT*
W/BM	M	A	DISTRES		BLG/YM	F	A	STBX*	
W/BM	F	J		FT*	BDG/YM	M	A	STBX	FT*
Y/MW	M	A	DISTRES		WY/RM	M	A	ROBMOB*	
R/MW	F	A	DISTRES		WR/RM	F	A	ST--	FT*
DG/MW	M	A	DISTRES		WLG/RM	M	A	BKBMOB*	
W/MY	F	A	BKBMOB	FT*	WDG/RM	M	A	STBX	FT*
R/MY	F	A	STBX	FT*	YW/RM	F	A	STBX*	
B/MY	F	A	ALARM*		YR/RM	M	A	BKBMOB*	
W/MR	M	A	ALARM*		YDG/RM	F	A	STBX*	
Y/MR	M	A	BKBMOB		RW/RM	U	J		FT*
-					RY/RM	F	A	STBX	FT*
R/MR	F	A	BKBMOB		RLG/RM	F	A	ROBMOB*	
LG/MR	F	A	STBX	FT*	LGW/RM	F	A	ALARM	FT*
DG/MR	M	A	STBX	FT*	LGDG/RM	M	A	STBX	FT*
B/MR	F	A	ALARM*		LGB/RM	F	A	STBX	FT*
W/MLG	M	A	ALARM*		DGW/RM	M	A	NOTRAIN	
Y/MLG	F	A	ROBMOB*		DGR/RM	F	A	STBX	FT*

Appendix 3: continued

Bands	Sex	Age	Test		Bands	Sex	Age	Test	
R/MLG	M	A	ROBMOB*		DGLG/RM	F	A	STBX	FT*
LG/MDG	M	A	ROBMOB		DGB/RM	M	A	ST--	FT*
W/MB	M	A		FT*	BW/RM	M	A	STBX	
Y/MB	M	A	DISTRES		BLG/RM	M	A	STBX*	
R/MB	F	A	BKBMOB	FT*	WDG/LGM	F	A	ROBMOB	
DG/MB	F	A	BKBMOB		YR/LGM	F	A	DISTRES	
B/MB	M	A		FT*	RY/LGM	M	A	BKBMOB	
					RDG/LGM	F	A	BKBMOB	
LGY/LGM	M	A	ROBMOB		DGW/LGM	M	A	ALARM	
DGR/LGM	M	A	NOTRAIN		DGLG/LGM	F	A	BKBMOB	
DGB/LGM	M	A	NOTRAIN		BDG/LGM	M	A	ROBMOB	
WY/DGM	M	A	DISTRES		WR/DGM	M	A	BKBMOB	
WB/DGM	M	A	ALARM		YR/DGM	M	A	DISTRES	
YDG/DGM	F	A	DISTRES		RY/DGM	M	A	ALARM	
RLG/DGM	F	A	DISTRES		RB/DGM	F	A	ALARM	
LGW/DGM	M	A	STBX		LGY/DGM	M	A	STBX	
LGR/DGM	F	A	DISTRES		LGDG/DGM	M	A	DISTRES	
DGY/DGM	M	A	DISTRES		DGR/DGM	F	A	BKBMOB	
DGB/DGM	M	A	ROBMOB		BW/DGM	M	A	DISTRES	
BY/DGM	F	A	DISTRES		BR/DGM	F	A	NOTRAIN	
BLG/DGM	M	A	NOTRAIN		WDG/BM	M	A	ALARM	
WB/BM	F	A	ALARM		YW/BM	F	A	ALARM	
YR/BM	F	A	ALARM		YB/BM	M	A	NOTRAIN	
RW/BM	F	A	ALARM		RY/BM	M	A	ALARM	
RLG/BM	F	A	ALARM		RDG/BM	M	A	ALARM	
RB/BM	F	A	ROBMOB		LGW/BM	M	A	ROBMOB	
LGY/BM	M	A	BKBMOB		LGDG/BM	F	A	BKBMOB	
LGB/BM	M	A	ROBMOB		DGW/BM	M	A	NOTRAIN	
DGY/BM	F	A	NOTRAIN		DGR/BM	M	A	DISTRES	
DGLG/BM	F	A	DISTRES		DGB/BM	M	A	DISTRES	
BW/BM	F	A	DISTRES		BY/BM	F	A	STBX	
BLG/BM	F	A	BKBMOB		BDG/BM	M	A	BKBMOB	
WY/MB	M	A	ALARM		WR/MB	F	A	DISTRES	
M/R	F	A	STBX		M/DG	U	J		FT*
M/WY	F	A	NOTRAIN		M/WB	U	J		FT*
M/YR	U	J		FT*	M/YDG	U	J		FT*
M/YB	U	J		FT*	M/RW	U	J		FT*
M/YLG	M?	J		FT*	M/BLG	M	A	NOTRAIN	
WM/W	U	J		FT*	WM/Y	F	A	ROBMOB	
WM/R	F	A	ROBMOB		YM/W	F	A	ROBMOB	
YM/DG	M	J		FT*	RM/W	F	A	BKBMOB	
RM/R	U	J		FT*	RM/LG	F	A	ROBMOB	
LGM/W	F	A	NOTRAIN		LGM/LG	F	A	ALARM	
LGM/DG	U	J		FT*	LGM/B	U	J		FT*
DGM/W	U	J		FT*	DGM/LG	U	J		FT*
DGM/DG	U	J		FT*	DGM/B	U	J		FT*
BM/W	U	J		FT*	BM/R	U	J		FT*
BM/LG	U	J		FT*	WM/WLG	M	J		FT*

Appendix 3: continued

Bands	Sex	Age	Test		Bands	Sex	Age	Test	
WM/WDG	U	J		FT*	WM/YR	U	J		FT*
WM/YLG	U	J		FT*	WM/YB	U	J		FT*
WM/RY	U	J		FT*	WM/RLG	U	J		FT*
WM/RDG	F	A	ALARM		YM/WY	M	A	STBX	
YM/WR	F	A	STBX		YM/WLG	F	A	STBX	
Kowhai Bush									
WDG/WM	M	A	STBX		WB/WM	F	A	STBX	
YW/WM	M	A	STBX		YR/WM	M	A	STBX	
YLG/WM	M	A	STBX		YB/WM	M	A	STBX	
RW/WM	M	A	STBX*		RLG/WM	F	A	STBX*	
RLG/YM	F	A	STBX		WM/YW	M	A	STBX	
WM/DGW	M	A	STBX		WM/DGY	F	A	STBX	
Allports Island									
M/W	M	A	STBX*		M/LG	M	A	STBX*	
M/B	M	A	STBX*		M/WY	M	A	TRAIN*	
M/WR	F	A	TRAIN*#		M/YW	M	A	TRAIN*	
M/YLG	M	A	TRAIN*		M/LGW	M	A	TRAIN*	
M/LGY	M	A	TRAIN*		M/LGB	M	A	TRAIN*	
M/BW	M	A	TRAIN*		M/BY	F	A	TRAIN*	
W/M	M	A	TRAIN*		R/M	M	A	TRAIN*	
B/M	F	A	TRAIN*		WY/M	F	A	TRAIN*	
WR/M	F	A	TRAIN*		BW/M	F	A	TRAIN*	
YM/-	F	A	TRAIN*		Mrw/BDG+	F	A	STBX*	

TRAIN = training regimes used in designing regimes used on Motuara Island.
+ "rw" = single band split into two colours.

Appendix 4: Statistical results, and means (± se) for Motuara Island and Kowhai Bush robin body movements during stoat and box trials. Comparisons were between (A) one bird present at a trial with the average response where two birds were present; (B) trials where the stimulus (stoat or box) was presented first compared to second; (C) males and females in trials where both birds were present.

A	Wilcoxon Sign Rank			One bird present	Both birds present
	p-value	mean	se	mean	se
Motuara Island stoat trials					
Flights	0.428	5.10	0.66	5.90	0.82
Wing flicks	0.908	1.36	0.38	1.44	0.55
Hops	0.084	4.29	1.05	2.13	0.66
Motuara Island box trials					
Flights	0.634	5.67	0.83	5.17	0.66
Wing flicks	0.737	1.13	0.53	0.90	0.43
Hops	0.911	2.43	0.58	2.33	0.67
Kowhai Bush stoat trials					
Flights	0.298	10.33	3.84	16.14	2.55
Wing flicks	0.547	6.66	2.40	9.86	2.56
Hops	0.157	24.30	7.88	14.12	2.93
Kowhai Bush box trials					
Flights	0.871	6.33	1.45	6.06	0.91
Wing flicks	0.796	1.33	0.49	1.63	0.86
Hops	0.905	3.00	1.67	2.75	1.25

B		Stimulus first		Stimulus second	
	p-value	mean	se	mean	se
Motuara Island stoat trials					
Flights	0.668	7.78	0.89	8.56	1.48
Wing flicks	0.275	3.00	1.11	1.54	0.58
Hops	0.716	3.93	0.93	4.46	1.11
Motuara Island box trials					
Flights	0.346	7.21	0.75	8.87	1.47
Wing flicks	0.129	0.73	0.37	2.23	0.93
Hops	0.853	3.57	1.28	3.38	0.77
Kowhai Bush stoat trials					
Flights	0.570	25.12	6.33	30.83	7.58
Wing flicks	0.555	14.62	6.03	20.00	6.27
Hops	0.102	19.00	3.39	27.70	3.36
Kowhai Bush box trials					
Flights	0.783	10.0	1.72	9.16	2.55
Wing flicks	0.105	3.88	1.64	0.50	0.22
Hops	0.569	5.25	1.62	3.33	3.14

Appendix 4: continued.

C	p-value	Male mean	se	Female mean	se
Motuara Island stoat trials					
Flights	0.055	5.86	0.88	3.79	0.85
Wing flicks	0.441	1.15	0.64	1.14	0.99
Hops	0.507	1.50	0.37	2.00	1.08
Motuara Island box trials					
Flights	0.917	4.64	0.95	4.65	0.64
Wing flicks	0.600	0.85	0.78	0.78	0.39
Hops	0.953	2.50	1.28	2.29	1.08
Kowhai Bush stoat trials					
Flights	0.266	17.91	3.45	14.36	2.43
Wing flicks	0.759	8.83	3.02	10.5	2.84
Hops	0.308	8.60	2.10	13.61	2.49
Kowhai Bush box trials					
Flights	0.327	4.88	1.01	7.25	1.53
Wing flicks	0.059	0.38	0.37	2.88	1.67
Hops	0.273	0.75	0.41	4.75	2.56

Appendix 5: Unpublished report to the Department of Conservation on the visit to Allports and Motuara Islands, 1989.

ALLPORTS ISLAND

TIME ON ISLAND: 15/9/89 to 3/10/89; 18 days
20/10/89 to 25/10/89; 5 days
19/12/89 to 23/12/89; 5 days

CAMPSITE: Three campsites in a gully above the small beach on the northwest side were used. The middle site, approx. 20m asl., was preferred as it was both close to the beach and out of sight of passing boats.

WATER: Seepages were available in the camp gully and in the large gully on the eastern side at beach level. This spring/summer was apparently wetter than usual and during long dry periods no water would be obtainable. Fresh water was carried for drinking supplies.

ROBINS: The season was already well under way by the time we arrived on the island. However, nesting was asynchronous with some pairs incubating, while others were only at nest-building or pre-nesting courtship phases. The majority of pairs had first nests built by late September. The earliest hatch date was
c.25/9/89. Given an incubation period of c.18 days then laying commenced on about 5/9/89.

In total, 25 nests from 21 pairs were found and 2 other pairs were known to successfully fledge chicks.

Three pairs renested for a second time after successfully fledging first nests. On 20/12/89 all three had chicks, one hatched on 19/12, one was mid-aged, and the third fledged on 22/12.

NEST FATE: Five nests failed to hatch, but of the nests known to hatch all successfully fledged at least one chick (except one of unknown fate). Causes of nest failure were;

1) abandoned ... 1 nest (1e)
2) died at hatching ... 1 nest (3e)
3) fell from trees ... 2 nests. One (2e) was blown down during a strong nor'wester, while the other (2e) was tipped from the crown of a large tree fern by new fern growth.
4) unknown causes ... 1 nest with contents missing but nest lining left tidy.

CLUTCH SIZE: Of the 16 first nests of known clutch size 14 (87.5%) had two eggs, the others being 1e and 3e clutches.

POPULATION: I estimate that there are 56 adult robins on the main island. There are 24 males and 17 females banded and I know of a further 11 unbanded (ub) females and 4 ub males. Using an island size of 16ha there is approx. 1.75prs/ha or 1pr/0.57ha.

DEAD ROBINS: Three dead adult robins were found on 20/9, 22/9, and 1/10 near traps 16A, 5C, and 11A respectively. The first two had been dead for 3-7 days but the third bird (a female) was found within one day of its death. The weather for the week prior to the finds was not exceptionally cold or wet. There is a strong possibility that robins ingested the poison baits used during the mouse eradication programme on the island. Baits were often dragged from their protective covers by opossums and remained in small fragments on the ground for several days; robins have been observed feeding around such areas.

MOTUARA ISLAND

TIME ON ISLAND: 26/10/89 to 19/12/89; 54 days

CAMPSITE: 100m north of jetty amongst large pine trees at the old homestead site. A brick

chimney still stands on site. The inflatable boat was kept above high water on the beach to the north of camp. Generally the campsite was excellent, being very sheltered from the prevalent nor'west and southerly winds. Some of the strongest winds in the area for some years occurred during my stay, with a southerly of 100+ knots being recorded at Cape Jackson being the worst of these. The pine trees around camp, although providing shelter, have been ring-barked and are now partially decayed. As a consequence some large branches fell near camp during high winds.

WATER: There was no suitable water supply on the island. Several small seepages (one of the largest was in the gully directly north of camp) were heavily polluted by penguins and sooty shearwaters. Water was collected approx. weekly from Ship Cove (1.5km away) in 20 litre plastic containers, using the inflatable boat.

ROBINS:

BREEDING: When we arrived on the island the stage in breeding cycle was highly variable. Many pairs already had fledged chicks on 26/10. Given an estimated age of two weeks since fledging, most of these pairs would have begun incubation during the first week of September.
A (second?) peak in laying occurred from the third week of October to the first week of November 21 of the 48 nests found were laid during this period.

The latest dates for the start of incubation were two nests on 21/11 and 23-24/11. The last nest to hatch did so on 12/12. Given a fledging period of c.21 days this nest would fledge on 2/1/90. The period from fledging to independence was not determined, but 2 chicks which fledged on 26/10 were still being fed by both parents on 18/12, a period of 53 days.

CLUTCH SIZE: The nest contents were determined for 10 egg and 29 chick nests. The average number of eggs/nest was 2.1, range 1-3. The average for chick nests was 1.4 chicks/nest, range 1-2.

NEST FATE:	number	% of nests
nests failed to fledge young *	18	37.5%
successfully fledged 1+ young	26	54.2%
abandoned before completion	1	
not fledged by 19/12	3	
TOTAL	48	

Causes of nest failure: (* from above)	number		% of tot nests(48)
1) predation, 6 definite and 3 probable	9		18.8
2) desertion; a) infertile eggs	4 }		
b) intraspecific fighting 1 }		12.5	
c) interspecific fighting 1 }			
3) unknown causes	3		6.3
TOTAL	18		37.5

2b involved two robin pairs with nests 9m apart who were continually fighting along their common boundary. The male of one nest was twice seen to fly up onto the rim of the other nest and drive the female it. Both nests were subsequently abandoned.
2c This nest was apparently abandoned after the incubating female was chased and pinned down on the ground by a very agressive male bellbird during the last of several interactions seen between the two birds.

Fate of nests with eggs: The fate of 46 nests where females were incubating was determined. A total of 34 (73.9%) hatched and 12 (26.1%) failed. Of those that failed 6 were abandoned (see above) and 6 were predated, most probably by Kiore, *Rattus exulans*.

Fate of nests with chicks: Of the 34 nests that hatched 26 (76.5%) fledged at least one young. Five (14.7%) failed and 3 had not fledged by the time I left the island on 19/12. Three of the chick failures were considered to be due to Kiore and 2 were of unknown causes.

MOULT: First moulting bird was a non-nesting female caught on 11/11. Most non-nesters were moulting by late November, and some adults feeding young fledglings had also begun to moult primaries by mid-December.

POPULATION: A total of 288 birds are now individually banded on the island, 196 of these are adults. In addition I estimate that there are up to 50 unbanded adults, giving an adult population of about 250. With an island size of 58.7ha then there are c.2.5 prs/ha or 1 pr/0.39ha. By the end of next season I will be more certain of numbers of pairs, territory size and total population.

NOTES ON BIRD SPECIES RECORDED DURING VISIT

A: ALLPORTS ISLAND

ROBIN.....see text.
GREY WARBLER.....throughout, est.10 pairs.
FANTAIL.....throughout, est. 5-10 pairs. 1pr with 3 just hatched chicks 30/9/89, dependent fledglings seen 21/12, 1 black phase camp gully 22/12.
SILVEREYE.....throughout, max. flock = 6.
SHINING CUCKOO.....1 heard 21/10.
TUI.....1 heard camp gully 21/12.
CHAFFINCH.....mod. numbers, 1pr nest-building 18/9.
GOLDFINCH.....throughout, heard in low numbers.
DUNNOCK.....1 at 23D trap 2/10, 2 on ridge top 23/10.
REDPOLL.....1 on 24/09 in 33 trapline gully.
BLACKBIRD.....few throughout, very timid.
THRUSH.....as for blackbird.
STARLING.....1 or 2 seen most days around the island, flocks of 5-c.100 seen and heard! flying over island each evening to roost sites on Motutapu and area of mahoe on northeastern corner of Allports.
WESTERN WEKA.....generally quiet and cryptic, single birds seen or heard in most areas between 15- 22/9. None heard during December trip.
PARADISE DUCK.....1pr flying past on 23/10.
MALLARD DUCK.....1pr in camp bay 20-23/10.
BLACK OYSTERCATCHER.....1 seen overhead 29/09.
REEF HERON.....1-2 regularly seen flying around island and feeding in inter-tidal. 6 flushed off rocks on se. side of Motutapu on 23/12 (wind nw.20-30 knots).
LITTLE SHAG.....single birds seen 16-18/9, 23/9, 20/12, all pied phase.
PIED SHAG.....1 on s. side 20/12, 23/12.
SPOTTED SHAG.....single birds seen around island, regular flight path n. in mid-channel in late evening - max. count 36 on 22/9.
BLACK BACK GULL.....regular around island in day and night, max.=16 on 24/9.
GANNET.....max.= 23 with fluttering shearwaters 30/9.
WHITE FRONTED TERN.....few seen regularly, usually gps of 2-6.
SKUA sp.....1 (probably Pomarine) chasing wftern 20/10.
FLUTTERING SHEARWATER.....regular, max. =c.200 off se. coast on 30/9, often heard flying over island at night, especially during rough weather but not seen on ground.
SOOTY SHEARWATER.....occasionally heard overhead at night.
LITTLE BLUE PENGUIN.....common and breeding, occupied burrows seen on 18/9, prs of birds seen in burrows during day on 20/9 and 21/9, two

birds found incubating 2e on 30/9 + 3/10

B: MOTUARA ISLAND

ROBIN.....see text.
GREY WARBLER.....very rarely heard, 5 records all in s. half of island Oct-Dec.
FANTAIL.....1 black juv? 30/11, 1 pied juv 6/12, 2 pied juvs 16/12 being chased by male robin.
BELLBIRD.....Abundant throughout, nests found from 20/11, first fledged chicks seen 3/12.
NZ PIGEON.....common, 5 nests found throughout island. earliest = eggs on 24/11, 1 hatched on 2- 9/12, 1 failed ?predation, and 3 still sitting on 19/12. 1-3 birds often seen flying to different bays on mainland through day time, and returning at dusk.
SILVEREYE.....few, mostly heard in lower scrubby areas.
SHINING CUCKOO.....1 heard 26/10.
WELCOME SWALLOW.....2 hawking insects, west side 19/12.
CHAFFINCH.....mod. common throughout, freshly dead male found near camp 22/11.
GOLDFINCH.....max. = 3 in camp pine trees 11/12. 1 chased over sea for 50m by bellbird 30/11.
REDPOLL.....occasionally heard.
BLACKBIRD.....mod. common, shy.
THRUSH.....less common than blackbirds, also shy.
STARLING.....nesting in cliff areas in mid w.,n.tip, and mid e. slopes in low numbers, ?c.20prs.
HARRIER HAWK.....1 pr on 28/10, 13/11, 2/12; single birds 18/11, 29/11, 10/12. All either over island or out to sea.
PARADISE DUCK.....1 pr flying sth over island 3/12.
BLACK OYSTERCATCHER.....1 pr regular between jetty beach + Ship Cove.
REEF HERON.....max seen = 2, regular over whole period.
LITTLE SHAG.....2 on jetty 30/11-4/12, pied + smudgy phase.
BLACK SHAG.....1 on 27/10.
PIED SHAG.....1 pr sth side 26/10, 1 pr with large fledglings seen in camp bay 24/11-4/12, regular at sea.
SPOTTED SHAG.....often seen flying past, 1-3 feeding within c.50m of shore most days, regular roost site on mid eastern side 6-10 birds.
RED BILLED GULL.....1 on jetty 28/11.
BLACK BACK GULL.....56 in Ship Cove area 29/11, 46 following fishing boat, otherwise <15 seen at any one time.
GANNET.....14 on 29/11, 23 on 4/12, otherwise <6 seen off western side of island at any one time.
WHITE FRONTED TERN.....few flying by feeding, max = 10 off s. coast 26/11.
CASPIAN TERN.....1 on 17/12 and 19/12.
FLUTTERING SHEARWATER.....heard most nights flying overhead, one found on ground in gully near camp 26/11, small rafts occasionally seen, c.50 on 26/11 Ship Cove, 48 on 29/11 s.coast. 25+ burrows in tussock on ntheastern tip thought to be this species.
SOOTY SHEARWATER.....10-20 birds on ground nightly around camp from 26/10 to c.4/11 followed by a quieter period with few birds landing, general increase in activity from c.20/11 onwards. 1e + bird in burrow on 29/11 but on 18/12 burrow taken over by moulting penguin. Groups of 5-10 burrows found in at least 3

other areas.
LITTLE BLUE PENGUIN.....eggs, small and large chicks and fledged young seen in late Oct. Large # of birds breeding over whole island including to within 5m of main ridge, up to 11 birds seen in lower camp gully in early evenings. Moulting birds regularly seen by 15/12, while others still had chicks.
GIANT PETREL.....1 seen 14/12.
PROCELLARIA spp.....1 seen 14/11.

Appendix 6: Unpublished report to the Department of Conservation on the visit to Motuara and Long Islands, 1990.

MOTUARA ISLAND: 21/09/90 to 20/11/90; 60 days

PEOPLE PRESENT: S.Bulman, L.Chadderton, R.Mulligan, S.Tulloch, J.Warham & N.Wells, (University of Canterbury); and Bill Cash, Kath Walker, (Dept. of Conservation), spent up to 10 days on the island. Lindsay Chadderton spent one month working on Robins with me.

CAMPSITE AND WATER: As for earlier reports.

GENERAL: A D.O.C. kiore eradication programme was well under way by the time of my arrival on the island. Most, if not all, kiore were eradicated by early September. D.O.C. personnel had cut and marked a 50m grid track system, with numbered poison bait tunnels at intersecting grid points. The track system was used extensively by us. It enabled detailed coverage of all areas of the island and accurate location of nests and non-breeding pairs.

ROBINS:
Breeding: My estimate of initiation of first-nests in the 1989 season was c.5/9/89 on Allports Island, and the first week of September on Motuara Island. On the basis of this I expected most nests to have eggs, or young chicks on my arrival (21/9/90). However, 10-15 pairs had already fledged young by 21/9, giving a lay date of about the first/second week of August, one month earlier than expected.

There were two main laying periods. Of the first 55 nests found, 34 had chicks of mid-old ages indicating a lay date of around the middle of August. A total of 15 of the first 21 egg nests did not hatch, and were most probably infertile. Three of these nests had odd-shaped eggs, and one was incubated for more than 30 days without hatching. Of the remaining 87 nests found, all but 9 were found at the nest-building, or incubation stage.

In 1989, very few pairs renested after successfully fledging young, or after nest failure.

In 1990, at least thirty pairs had commenced renesting, after successfully fledging young, by the time I left the island. A few pairs had raised first clutch fledglings and were already feeding chicks in second nests by 15/11/90.

NEST FATE

A: Nests with eggs when found (n=102)		
# nests failed to hatch	35	41.7% (% all of 84 nests of known fate)
# successfully hatched	49	58.3%
# fate unknown	9	
# abandoned before completion	1	
# not hatched by 19/11	14	
Fate of egg nests that failed to hatch (n=35)		
# did not hatch, reasons unknown	9	
# deserted	14	16.7%
# lost eggs during incubation	8	9.5%
# tipped out by punga growth	3	3.6%
# fell from tree	1	1.2%
Fate of egg nests that hatched (n=49)		
# not fledged by 19/11	33	
# fledged	11	
# failed to fledge	4*	
# fate unknown	1	

B: Nests with chicks when found (n=41)

# nests that failed to fledge	4*
# successfully fledged	32
# fate unknown	5

Cause of failure of chick nests.

All nests that failed to fledge chicks (* n=8) were found with dead chicks in nest following cold wet weather conditions. All chicks were c.5 days of age.

PREDATION ON EGG NESTS

Eight nests lost eggs during incubation, and two deserted nests also lost eggs. There was no set appearance of a nest following predation. Nests had "predation sign" ranging from a 40mm hole in the bottom of the nest, to tidy lining no eggshell, to messy lining no shell, to 10-15 pieces of small shell, to 1 untouched egg + a half shell, to both eggs with a large hole in the side!

The latter nest was sent to Rowley Taylor (DSIR Nelson) who considered that it was possible that it was eaten by a rat (although, no poison baits were being taken by the time of my visit, indicating that most (all?) rats were eradicated).

Predation by Harrier Hawks, or Moreporks is possible, although no moreporks were seen or heard during this trip.

MOULT

First moulting birds were caught on 17/11/90. They were a pair from a nest which was found on 29/9 with eggs, and had failed by 9/10.

POPULATION

Band Recoveries

Number banded 1989 or earlier		Seen Sept-Nov 1990	%recovered		%lost	
Pullus	30	6	20		80	
Juvenile	62	15	24.2		75.8	
Adult F	74	40	54.1		45.9	
Adult M	120	69	57.5		42.5	
Total Ad.	194	109	56.2		43.8	
Total	286	130	45.5		54.5	

Because of the good coverage of all areas of the island the total number of banded birds seen is almost certainly definitive. All banded birds were found by 25/10/90, one month after arrival. Pullus and juvenile losses were highest, but adult mortality was still very high at around 43%.

A sample of banded birds were sighted in July, by myself, and in August, by DOC staff. Of 88 individuals sighted in July, 37.5% were not seen in October. Of 58 individuals seen in August, 37.9% were not seen in October.

Losses of this level in a two month late winter-early spring period seem to be very high. The eradication of kiore, with its associated availability of poison cannot be ruled out as a cause of high mortality. However, mortality may be naturally high during this period in some years. More effective long-term monitoring before an eradication campaign will provide more complete answers as to the effect of such campaigns on bird populations.

CURRENT POPULATION

The territorial nature of robins, a high percentage of banded birds and an effective track system means that it has been possible to accurately estimate the total population of robins on Motuara Island.

A total of 150 nests of 133 pairs were found. Nests were not found for 19 pairs who had fledglings and for 15 pairs that were "stuffing" (= failed first time nesters, late breeders and non-nesters). About 26 single males (batchelors) were also found. Some of these males defended territories, while others wandered over several ha.

Total population = 167 pairs + 26 batchelors = 360 Adults.
Island size of 58.7 ha gives 2.8 prs/ha or 1 pr per 0.35ha.

SOOTY SHEARWATER - VEGETATION STUDY:

This work is progressing well. Five exclosure quadrats were shifted to a north-eastern group of burrows after Little Blue Penguins were found using experiment burrows prior to the arrival of the Shearwaters.

The establishment, growth and survival of seedlings in exclosures, outside burrows and in areas away from burrows is being monitored by photography, and by plotting seedling co-ordinates on a grid at approximately three monthly intervals. Burrow occupancy and shearwater activity was also monitored. Most of Motuara and Hippa Islands were searched for active burrows during the day and in the early evening.

A small experiment, examining the effect of shearwater excreta on individual five finger seedlings, was set up near the camp site. Seedlings were smeared with excreta at regular intervals (controls were not smeared) and stem height, leaf number, leaf surface area and plant survival was monitored for seven weeks.

Visits to Motuara Island to continue this work will be made in late January and in July.

LIZARDS:

Two species of skink were seen this season (no skinks have been seen previously). A small *L.nigraplantare* type was regularly seen in sunny spots along the main ridge, and along the shoreline on the western side.

Two larger skinks were seen. One seen on 22/10/90, 10m north of the 31X-beach track (= south end of the jetty beach) and the other 50m north of the camp, again just above the shore.

A description of the first is as follows:

Body - above, light speckles on a pale brown background
side, black with light coloured spots
Tail - brownish, stubby
Generally wide bodied. About 130mm long.
Possibly *L.infrapunctatum* ?

LONG ISLAND: 6/11/90 to 7/11/90

R.Maloney & N.Wells

Much of the main ridge and 1/3 of the eastern side of the island was briefly searched for robins. Two pairs were found. One pair was nesting (just hatched) 30m e. of the main ridge down from the bunkers and water tanks. The male was banded WW/MW. An unbanded male with an unbanded juvenile were found at the south east end of the shingle spit on the western side of the island. No banded birds were seen. In addition to the bush and shorebird species list for Motuara Island three other species were seen. These were tomtit, tui and rock pigeon. No kiwis were heard from the shingle spit over night.

NOTES ON BIRD SPECIES RECORDED DURING VISIT:

MOTUARA ISLAND

ROBIN.....see text.
GREY WARBLER.....rare, but more common than last year. Birds attracted to alarm call experiments on two occasions.
FANTAIL.....1 pr with juv. near trap 191. Seen around traps 112-130 & 32D-31E.
BELLBIRD.....Abundant throughout, nest-building seen by 10/11.
NZ PIGEON.....common, movements as 1989.
SILVEREYE.....few, mostly heard in lower scrubby areas.
SHINING CUCKOO.....first heard 1/10, daily to 8/10, sporadically after that.
WELCOME SWALLOW.....2 hawking insects, n.tip 9/11.
CHAFFINCH.....mod. common throughout.
GOLDFINCH.....two at n.tip 9/11.
REDPOLL.....occasionally heard.
BLACKBIRD.....mod. common, shy. 5 dead blackbirds found.
THRUSH.....less common than blackbirds, also shy.
STARLING.....mod. common in mahoe/kohekohe forest areas.
HARRIER HAWK.....1 pr resident, seen all over island. Roost site on north tip contained pellets with sheep wool, beetles, rat/mouse fur.
BLACK OYSTERCATCHER.....1 pr regular between jetty beach + Ship Cove.
REEF HERON.....max seen = 2, regular over whole period.
BLACK SHAG.....occasional.
PIED SHAG.....regular at sea and roosting around island.
SPOTTED SHAG.....often seen flying past, 1-3 feeding within c.50m of shore most days, regular roost site on mid eastern side 6-10 birds nesting). Also 2 nests on north-western side.
KING SHAG.....2 off n.tip on 21/9. One off south coast 1/10. One in Ship Cove, c.10/10.
RED BILLED GULL.....few at sea.
BLACK BACK GULL.....following fishing boats, otherwise <15 seen at any one time. Nesting Long Island.
GANNET.....<6 seen at any one time.
WHITE FRONTED TERN.....few flying by, feeding.
CASPIAN TERN.....occasional.
FLUTTERING SHEARWATER..heard most nights flying overhead, small rafts occasionally seen, c.300 on 4/10 500m n. of island. 100+ came into burrows on n.tip at 1930h.
SOOTY SHEARWATER.....10-20 birds on ground nightly around camp. Burrow occupancy, and burrow location will be written up at a later date.
LITTLE BLUE PENGUIN.....Large # of birds breeding over whole island including to within 5m of main ridge, up to 11 birds seen in lower camp gully in early evenings. Birds on eggs 21/9. Young chicks by mid-Oct.